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ENVIRONMENTAL CORRELATES OF SPATIAL VARIATION IN SPAWNING ABUNDANCE OF BULL TROUT (*Salvelinus confluentus*) IN ROCK CREEK BASIN, MONTANA, USA

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ABSTRACT

INTRODUCTION

The variation among streams in the population abundance of fishes should logically provide some measure of the effects of land use disturbance and other landscape factors on population status. Rieman and McIntyre (1996) examined spatial and temporal variability in bull trout (*Salvelinus confluentus*) redd counts and found subtantial stream-by-stream , but they did not examine environmental or biological correlates of this variation. Baxter et al. (2000), used the rate of change in redd counts of bull trout to compare populations among the principal spawning tributaries of the Swan River Basin, finding bull trout populations to be positively correlated with a metric describing downstream flux in valley width that influences vertical flow exchange, and inversely correlated with road density of the contributing catchment area. At a larger regional scale, Rieman et al. (1997) found that bull trout in the Columbia River Basin were more likely to occur in watersheds with low road densities.

In the studies cited above and others of this kind, metrics of human disturbance (such as road density, considered a general index of human disturbance and intrusion [Trombulak and Frissell 2000]) and some measure of natural environmental variation (e.g., in elevation, stream size, temperature, or channel geomorphology) both typically weigh heavily in the correlations. This indicates that in many cases the effects of human disturbance may be obscured (or alternatively might appear exaggerated) by the background or interactive effects imposed by natural environmental variation among streams. In a sense, long-term natural factors such as catchment and channel geomorphology or hydrology may be seen to determine the potential capacity (*sensu* Frissell et al. 1986, Ebersole et al. 1997) of a given stream to support fish of a given species, with human alterations causing departure from that naturally determined limit. Few studies have established the magnitude of variation that can be expected among streams as a function of natural environmental factors and of human disturbance, but establishing the natural pattern of potential population abundance is essential to ascribing observed patterns in fish abundance to landscape alteration or other effects of recent human activity (Platts 1979, Frissell et al. 1986), and will also be necessary for effective diagnosis and treatment of causes of habitat disruption (Ebersole et al. 1997). This is especially crucial if natural factors and human effects have similar magnitudes of effect of population abundance.

All observational metrics of fish population abundance are subject to substantial error, but they vary in methodological difficulty thus data availability. Redd counts to estimate spawning abundance are widely employed for bull trout and other salmonids because they rely on visual observations that are quickly conducted over large reaches of stream. However, redd counts may be subject to large error, especially variability among observers in the identification of redd locations (Dunham et al. 2001). Despite such limitations, Baxter et al. (2000) successfully used such data to resolve differences among tributaries that could be related to environmental factors. While error in redd counts remains problematic and warrants much closer attention, we assume that as long as surveys conform to certain basic methodological criteria, the typical variation in magnitude in linear redd density (standardized by stream length surveyed) approaching two orders of magnitude is great enough that redd counts should roughly indicate whether a streams is high, intermediate, or low in spawner abundance relative to neighboring streams in the same river basin.

The approach of comparing redd counts among streams in a river basin also assumes that bull trout populations in neighboring streams are demographically independent units and can be analyzed as such statistically. While the ecological literature has examples of significant spatial autocorrelations in bull trout occurrence (Reiman and McIntyre 1996, Dunham and Reiman 1999), and these have often been interpreted as implying dynamic exchange of individuals occurs within a metapopulation context (*sensu* Hanski 1994, Wiegand et al. 1999), recent genetic analyses tend to support the hypothesis that there is little apparent genetically effective, contemporary exchange among bull trout populations inhabiting even closely neighboring tributaries (Kanda and Allendorf 2001, Spruell et al. 2001). These findings suggest that previously reported spatial correlations (Rieman and McIntyre 1996, Reiman et al. 1997, Dunham and Reiman 1999) are more likely a consequence of spatial coherence in environmental factors that determine variation in abundance than of dynamic inter-population exchange of individuals. Nevertheless, a first-order test of the question of spatial autocorrelation can be conducted in any such analysis by incorporating a simple, nearest-neighbor metric as an independent variable into the model.

The present study is an exploratory analysis of spatial variation in bull trout redd counts in tributaries of an important stronghold of this federally listed species in the Upper Clark Fork Basin of Montana. Using simple correlation models, we investigated the strength of observed relationships between redd counts and a host of environmental metrics reflecting the climate, lithology, geomorphology, and human management history of tributary catchments. We also explore the possible interaction of natural and human factors by stratifying our analysis by the natural factors accounting for most of the variation among sites. Unlike previous studies at a similar scale, (e.g., Hillman and Watson) we considered a basin with relatively high-quality populations and habitats, with extensive natural areas and a mainstem stream only moderately altered by human activity.

STUDY AREA

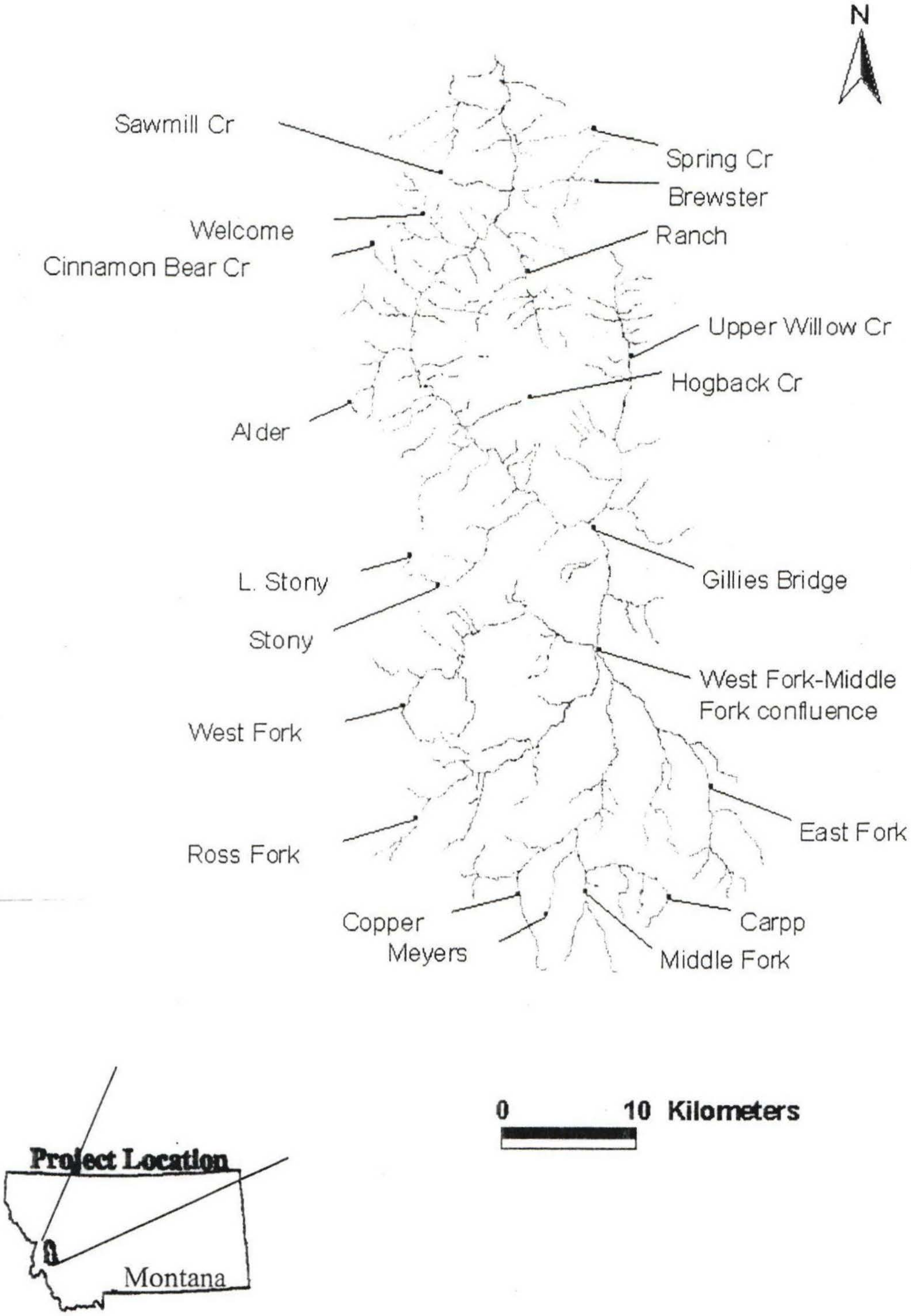
Rock Creek, a sixth-order, generally north-flowing tributary to the Clark Fork of the Columbia River near Clinton, Montana, drains an area of 2,292 km^2 with an annual mean discharge of 15 m^3/sec (530 ft^3/sec; USGS 2000) (Figure 1). Eighty-three percent of the drainage is in public ownership: 80% Forest Service, 2% Bureau of Land Management, and 1% State (MBTSG 1995). Private lands in the drainage consist largely of agricultural ranch lands, although residential development is increasing. Basin elevations range from 1,072 m at the mouth to 3,187 m at Warren Peak. Eighty-five percent of the Rock Creek drainage is in the metasedimentary geologic district, 13% is granitic, and 2% is volcanic (Jensen 1998). The region of primarily volcanic parent material occurs in a single polygon to the west of the Rock Creek mainstem and north of the confluence of the West and Middle Forks. Two areas along the western boundary of the drainage comprise the granitic district. The remainder of the drainage is in the metasedimentary district (Jensen 1998). Fluvial geomorphology comprises 61.8% of the drainage area, alpine glaciated lands 35.5%, alluvial lands 1.5%, and fluvial/lacustrine lands 1.3% (Jensen 1998). Most of the upper (southern) end of the drainage and a smaller area along its western boundary comprise the alpine-glaciated geomorphic class. The alluvial class is confined to the Upper Willow Creek catchment. Fluvial/lacustrine lands influenced by Glacial Lake Missoula are limited to the lower (northern) end of the drainage near Rock Creek's confluence with the Clark Fork. The remainder of the drainage falls into the fluvial geomorphic class (Jensen 1998).

Upper and lower portions of the Rock Creek drainage (above and below Stony/Little Stony Creek subbasins) differ substantially in character, with upper drainage tributaries tending to be longer, lower-gradient, having smaller proportions of subbasin areas in steep slope classes and extensive areas in wide valley bottoms of glacial or alluvial fill, often with limited canopy cover. A large portion of the upper drainage was alpine-glaciated, versus only a few small headwaters areas in the lower drainage. Proportion by area of granitic rock types is generally higher in the upper basin.

The Rock Creek drainage has had relatively few human impacts compared to other similar- size drainages in western Montana (MBTSG 1995). Past human-related disturbances considered to have impacted bull trout in the drainage include mining, timber harvest, road building, agriculture, and residential development (MBTSG 1995). East Fork Reservoir Dam is an impassable upstream migration barrier, which isolates a bull trout population in the reservoir and its tributaries (USFS, unpublished data). Highly valued aquatic resources and recreation opportunities have focused considerable public attention on the drainage (Knox et al. 1991). Several conservation easements have been established on private lands (Goldman 1997). Public concern over Rock Creek prompted the Deer Lodge and Lolo National Forests to suspend timber harvest activities within the drainage in 1991 until completion of a cumulative effects analysis. MBTSG (1995) stated that Rock Creek and the Blackfoot River are the only areas of the Upper Clark Fork basin where the fluvial migratory bull trout life history persists, and that all other Upper Clark Fork basin bull trout are resident fish isolated in headwaters areas by mining pollution and other habitat degradation in the upper Clark Fork. Other evidence suggests a remnant fluvial migratory component may persist in other isolated areas of the Upper Clark Fork Basin (Eric Reiland, Montana Fish, Wildlife and Parks [MFWP], personal communication).

Redd counts beginning in 1993 document bull trout spawning efforts in 19 tributaries within the Rock Creek drainage (Beaverhead-Deerlodge and Lolo National Forests, unpublished data). In addition to East Fork Reservoir, Kaiser and Moose Lakes in the upper Middle Fork basin are reported to contain migratory bull trout (MBTSG 1995). Unpublished MFWP data collected in 1959 also record bull trout presence in Bobcat, Cougar and Little Hogback Creeks, all tributaries to the Rock Creek mainstem (MBTSG 1995).

Figure 1. Rock Creek study area


N
Sawmill Cr
Spring Cr
Brewster
Welcome
Ranch
Cinnamon Bear Cr
Upper Willow Cr
Hogback Cr
Alder
Gillies Bridge
L. Stony
Stony
West Fork-Middle Fork confluence
West Fork
East Fork
Ross Fork
Copper
Carpp
Meyers
Middle Fork
0
10 Kilometers
Project Location
Montana

METHODS

Forest Service bull trout redd surveys have been conducted in Rock Creek tributaries since 1993 (Lolo and Beaverhead-Deerlodge National Forests, unpublished data). Survey effort has been variable among streams, reaches and years. Index reaches have been established in some streams with the goal of surveying them annually for bull trout population monitoring. We used these existing data to identify 19 bull trout spawning tributary "subbasins" within the Rock Creek drainage, which were our analysis units (Figure). To reduce the likelihood of basing conclusions on highly anomalous cases, we required a minimum of two years survey effort with no redds found to include a subbasin in our sample. If any redds were found in any survey year, the subbasin was included.

Fifteen of these subbasins each comprised the entire drainage area of a single named tributary. Six of these fifteen were nested within a larger subbasin that was also an analysis unit. The Ross Fork (tributary to the West Fork at km 0.3) was treated as a functionally independent "primary" subbasin. No redd-survey data were available for the East Fork (tributary to the Middle Fork at km 3.5) below an impassable dam, except in its tributary Meadow Creek. Therefore, the East Fork drainage was excluded for analysis from the Middle Fork subbasin, Middle Fork area and other attribute values were adjusted accordingly, and the Middle Fork above East Fork treated as a primary subbasin analysis unit. Meadow Creek was included as a separate subbasin unit. Three larger tributaries, the Middle and Ross Forks and Copper Creek, had sufficient redd-survey records to distinguish upper and lower subbasins with substantially different levels of spawning use (minimum 3 years survey effort both above and below the nested subbasin delineation pourpoint). For example, no redds were found in Ross Fork reaches two (surveyed in 1999 only), three (1996, 1997 and 1999) and four (1996 and 1997), comprising all the reaches surveyed below Falls Creek. Surveys in reaches five (1997-2000) and six (1997 and 1999) found redds in all survey years, with a maximum density of 3.0 redds/surveyed km in 1998 in reach five (only reach surveyed in 1998). On this basis, the Ross Fork drainage upstream of the Falls Creek confluence was delineated and classified "moderate/high" redd density with a maximum of 3.0 redds/km, and basin-scale candidate predictor variables were summarized for this delineated subbasin. Spawning use of Ross Fork below Falls Creek was classified "low/none", based on redd densities within only the survey reaches below Falls Creek, and maximum redd density was recorded as zero. However, basin-scale predictor variables for this analysis unit were summarized for the entire Ross Fork drainage, including the nested subbasin above Falls Creek, under the assumption that basin-scale influences would be cumulative in the downstream direction. The same procedure was followed for the Middle Fork and Copper Creek upper and lower subbasins. We did not attempt to evaluate or control for possible "nesting effects" in the analysis.

Watershed boundaries for subbasin analysis units were delineated from Digital Elevation Models (DEMs) in a Geographic Information System (GIS) at the Forest Service's Rocky Mountain Research Station (RMRS) from pourpoints we identified at the downstream limits of the subbasins. Total area of each subbasin was calculated in the GIS, and values of subbasin attributes (Table 1) were summarized for each subbasin using

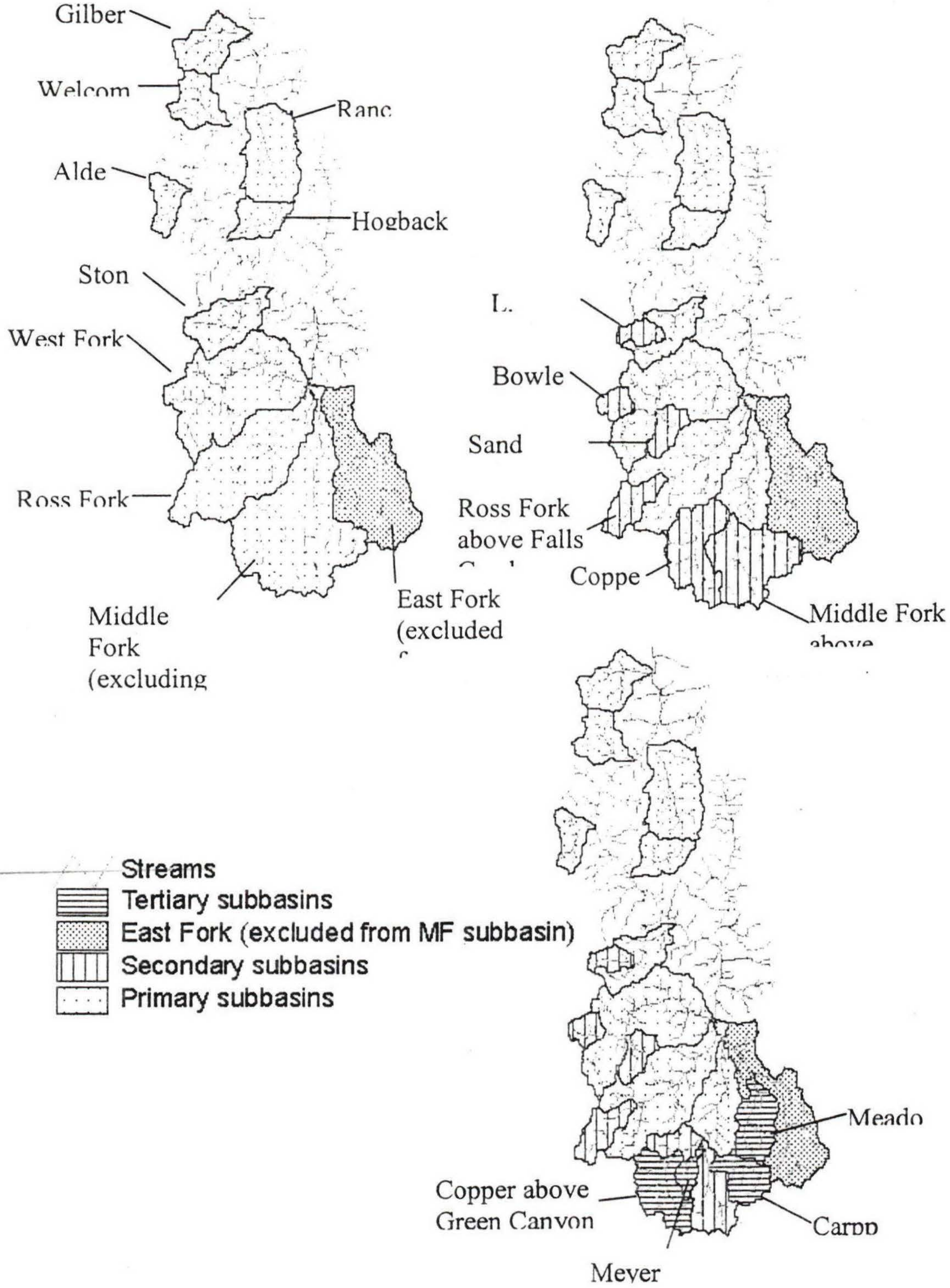
Arcview's tabulate areas function (Spatial Analyst extension), then exported to a spreadsheet for further analysis. Stream lengths and variables that were proportions of stream length rather than subbasin area were calculated from a routed GIS hydrography coverage and entered in the spreadsheet.

Candidate variable selection and analysis

We obtained existing GIS coverages or developed data sets from maps for basin/landscape-scale variables that we hypothesized or other studies have suggested are likely to influence quantity and quality of bull trout spawning habitat. We began with the assumption that variables used needed to capture environmental variation in several broad categories at landscape scales that would be expected to influence habitat attributes and bull trout spawning use at finer scales. These categories included geology, geomorphology, climate, stream temperature, spatial geometry, size, elevation, topographic relief, orientation and land use/management effects (Table 1).

We evaluated both untransformed and natural log-transformed values of all variables (natural log 1+x if data values of zero were present) for symmetry and approximation to normality of their distributions using histograms, normal probability plots, Kolmogorov-Smirnov and Shapiro-Wilk tests. We selected whichever of the untransformed or transformed variable best approximated symmetry and normality for further analysis (Table 1). Figures and text in Results consistently show and refer to the untransformed variables, while table summaries show the actual model input variable if a transformation was used.

Figure 2. Rock Creek drainage subbasin analysis units: primary, secondary (nested within primary) and tertiary (nested within secondary).


Gilber
Welcom
Ranc
Alde
Hogback
Ston
West Fork
Ross Fork
Middle Fork (excluding
East Fork (excluded
L.
Bowle
Sand
Ross Fork above Falls
Coppe
Middle Fork above
Streams
Tertiary subbasins
East Fork (excluded from MF subbasin)
Secondary subbasins
Primary subbasins
Meado
Copper above Green Canyon
Carpp
Meyer

We examined both Pearson and Spearman (nonparametric) correlation matrices of all candidate predictor variables and redd density metrics to check for significant monotonic but nonlinear associations among variables. The two matrices were very similar and we considered only Pearson correlations in further analyses (Appendix A).

We used both simple and multiple regression analyses to examine associations with redd densities of candidate predictor variables and combinations of predictors. We performed analyses on the complete data set of 19 subbasins, as well as on two-level stratifications of the data set by several of the landscape-scale variables (e.g. geomorphology, stream temperature). We stratified the data set to examine whether associations within a stratum might differ from those in the other stratum or in the unstratified sample, once the influence of the stratifying variable was accounted for.

We used strength of correlations with redd densities to evaluate candidate predictor variables for entry into stepwise and backward multiple regression model selection procedures. Some variable combinations were also directly entered into models to examine specific hypotheses. For example, land use/management variables (Table 1) were systematically entered individually with other candidate predictors to evaluate whether management effects not evident from correlations might become apparent with other effects accounted for in the model. We considered only the variable most-correlated with redd densities from within a landscape category (e.g. channel slopes at different scales, Table 1) as a candidate predictor in a particular analysis, except when testing a specific hypothesis regarding combinations of predictors. For example, maximum-redd-density-reach average channel slope was systematically entered into models with broader-scale average channel slopes (if the different-scale channel slopes did not correlate significantly with each other) to test a hypothesis that lower-gradient reaches nested within higher-gradient subbasins might be associated with higher maximum redd densities.

Pearson correlation and multiple regression analyses measure strength of linear association based on assumptions of normal distributions. Some of our variables deviated substantially from normality, even after transformation, and some were ordered categorical variables (e.g. stream order). Other variables, although continuous, had nearly binary distributions, especially within some strata after stratification. Johnson (1998) considers most multivariate methods quite robust with respect to nonnormal data and expects them to work well when variables can be quantitatively ordered in some way.

Limited sample size, especially after stratifications, raised concerns of overfitting (using too many variables to explain too few cases), further constraining our analyses and the strength of inferences we could draw from them. There were many significant correlations among candidate predictor variables as well (multicollinearity). Overfitting and multicollinearity may result in models that account for most of the variation in the response variable (high R^2) and appear highly significant statistically (small p-value), yet perform very poorly on new cases or data sets (SPSS 1999). To minimize this possibility, we applied several screens to models we report: 1) an absolute minimum of four times the number of cases as predictor variables in any model, to reduce risk of overfitting; 2) lack of significant correlation between predictor variables in the same model to avoid multicollinearity problems; and 3) p-values <0.05 for the model (ANOVA) as well as for coefficients of all predictor variables in the model. Condition one limited the number of predictors to four in analyses of the unstratified sample (n=19), and to two in analyses within strata (range 8-11). However, no models from the unstratified sample with more than one predictor met the other two conditions. We followed the same variable selection and model-fitting procedures within each stratum as for the unstratified sample (i.e. generate matrix of correlations within stratum; screen for strongest correlations with redd densities and lack of significant correlations among predictors in any model; screen resulting models and all predictor variables in them for significance at $\alpha=0.05$). All evaluations of statistical significance were at $\alpha=0.05$.

We examined simple or three-dimensional scatterplots of all models meeting the criteria just described. Where graphs suggested a single highly influential point was driving the relationship, we also examined influence statistics (Cook's D, standardized DfFits and standardized DfBetas). Common "rules-of-thumb" suggest flagging points as possibly influential if |Cook's D| > 4/n, |DfFits| > 2*SQRT(p/n) or |DfBetas| > 2/SQRT(n), where n is sample size and p is the number of parameters (including intercept) in the model (Dr. Jonathan Graham, Department of Mathematical Sciences, University of Montana, Missoula, personal communication). We do not report models that met our other criteria but had extreme values relative to these rule-of-thumb cutoffs for one or more subbasins. We do report models with cases exceeding cutoffs by relatively small amounts (e.g. statistic less than five times cutoff), noting the possible influence.

We also examined an additional stratification by location within the Rock Creek drainage that captured much of the variation in other landscape-scale attributes between upper and lower portions of the drainage. For example, a discriminant function analysis using subbasin proportion with slopes >46% and subbasin proportion alpine-glaciated discriminated with 100% success, in both the original classification and leave-one-out cross-validation, between subbasins below Stony Creek and those above and including Stony. Uneven sample sizes (n=5 and n=14), with the lower drainage sample too small for meaningful inference, and limited applicability beyond Rock Creek led us to abandon this approach.

Redd Density

Choice of appropriate scale for summarization/analysis of redd survey data is problematic. Numerous studies indicate bull trout spawn in only a small proportion of the stream length accessible to them. Different results may be obtained depending on whether redd counts are summarized by measured survey length within a single high-spawning-density area, by geomorphic reach length, total surveyed length within a stream, total count within a tributary drainage, larger basin or watershed, etc. We divided redd counts by the length of stream surveyed to provide a measure of control for variable survey effort among reaches, streams and years. We used maximum redd density (number of redds/surveyed stream length) recorded in a subbasin analysis unit in any survey year, summarized at two different scales (total surveyed length and individual survey reach), as a response variable representing level of bull trout spawning use. We reasoned that maximum single-reach-scale densities might better reflect the highest-quality spawning habitat within the subbasin, while surveyed-length-scale maximum densities might better reflect the overall production capacity and importance to the Rock Creek metapopulation of each tributary subbasin. We summarized maximum recorded redd densities at the individual-survey-reach scale by dividing number of redds reported for a reach by the reach length reported in Forest Service reach delineation lists, using the maximum value occurring in any year in any reach within a subbasin as the reach-scale response for that subbasin. At the surveyed-length scale, we divided the total redds reported within the delineated subbasin analysis unit by the total stream length surveyed the same year within that subbasin, using the maximum value from any year as the response variable.

Table 1. Candidate predictor (independent) and response (dependent) variables for modeling bull trout redd densities.

landscape category	variable name	description	
spatial	drngloc2	subbasin delineation pourpoint location, stream km above RC mouth	1:24K
	nearest	distance from subbasin delineation pourpoint to nearest known bull trout spawning tributary, km	1:24K
elevation	prpntele	subbasin delineation pourpoint elevation, feet	7.5' q
	avgelft	average subbasin elevation, feet	1:24K
	elev7ppn	proportion of subbasin area in elevation classes >7000 feet	1:24K
size	lntotlar	natural log total subbasin area	7.5' D
	lnstlnth	natural log stream length w/in subbasin, km (routed GIS hydrography)	1:24K
	pptorder	stream order at subbasin delineation pourpoint	[illegible]
	mxrrdord	stream order of maximum-redd-density reach	[illegible]
orientation	aspctcls	average stream valley aspect class, 1=N-S, 10=E-W	map
geology	metseppn	proportion subbasin area in metasedimentary geologic district	Jense
	grnitppn	proportion of subbasin area in granitic geologic district	Jense
	grnt2ppn	proportion of subbasin area in granitic rock types (higher-resolution)	Jense 1955)
	volcappn	proportion of subbasin area in volcanic geologic district	Jense
geomorphology	ln1BAVSl	natural log (1+stream length w/in BAVS in subbasin)	7.5' q
	BAVSppn	proportion of subbasin stream length within BAVS	7.5' q
	ln1kbB	natural log (1+(number of knickpoints below BAVS in subbasin))	7.5' q
	ln1kbBdn	natural log (1+(knicks below BAVS/stream length))	7.5' q
	BAVlnslp	proportion stream length in BAVS * natural log average subbasin channel slope	7.5' q
	fluvppn	proportion of subbasin area in fluvial geomorphic class	7.5' D
	flulappn	proportion of subbasin area in fluvial-lacustrine geomorphic class	7.5' D
	alluvppn	proportion of subbasin area in alluvial geomorphic class	7.5' D
	alpglppn	proportion of subbasin area in alpine-glaciated geomorphic class	7.5' D
	gemordum	dominant geomorphic class: 0=fluvial, 1=alpine-glaciated	7.5' D

Table 1 (continued)

landscape category	variable name	description	
basin relief	slope46	proportion subbasin area in slope classes >46%	7.5' D 1998)
channel slope	lnbsnslp	natural log average subbasin channel slope	7.5' q
	lnsrvslp	natural log average redd-surveyed channel slope	USFS 1998)
	lnmxrdsl	natural log maximum-redd-density-reach average channel slope	USFS 1998)
	lnmxrbsn	natural log (ratio max-redd-density-reach avg slope to subbasin avg slope)	USFS 1998)
climate	pcp32ppn	proportion of subbasin area in annual precipitation classes >32"	PRIS 1998)
	sr300ppn	proportion of subbasin area in solar radiation classes >300 W/sqr m	ICBE (RMR
	ln1mxt50	natural log (1+proportion of subbasin area in average maximum temperature classes >50F)	ICBE (RMR
land use/ management	ln1trls	natural log (1+trail density, km/sqr km)	1:24K
	ln1roads	natural log (1+road density, km/sqr km)	1:24K
	r_tdns	roads-trails combined density, km/sqr km	1:24K
	ln1sdsp	natural log (1+proportion of subbasin area in seedling/sapling class)	Beave deline
	brktrout	brook trout, 0=not reported, 1=reported presence	MRIS
	wldrlppn	proportion subbasin area designated wilderness/inventoried roadless NF	NRIS
stream temperature	lnm7msg2	natural log (1999 MWMT, degrees C) + model-predicted for missing	field d
	p7d98msg	1998 MWMT, degrees C, + model-predicted for missing	field d
redd density (dependent/ response variables)	mxrdddns	maximum recorded density, redds/km total redd-surveyed length in subbasin	USFS
	rddns3cl	redd density, 3 classes: <2/km, 2-5.99/km, >=6/km	USFS
	rddns2cl	redd density, 2 classes: <2/km, >=2/km	USFS
	ln1mxrrd	natural log (1+maximum single-survey-reach redd density)	USFS

DEM = Digital Elevation Model (GIS coverage) RMRS = USDA Forest
Service Rocky Mountain Research Station, Boise
CFF = Cartographic Feature File (GIS coverage)
ICBEMP = Interior Columbia Basin Ecosystem Management Project

Three exceptions were made to this procedure. In Gilbert Creek, the maximum recorded redd density was based on 2 redds in a survey of only 0.4 km of the delineated reach length (3.4 km) in 1996. Because this survey effort was so limited, we used the second-highest Gilbert Creek density as a response. Likewise, the highest density in Copper Creek consisted of 4 redds within a delineated survey reach of only 0.3 km. We combined that reach with the next upstream reach for this analysis. The 1999 relative distribution of redds between Stony Creek reaches two (44 redds, 14.39 redds/km) and three (3 redds, 1.33 redds/km) appeared anomalous and was likely due to misreporting of redd locations resulting from confusion over reach breaks. In all other years reach three had at least as many redds as reach two, and usually many more. Because of this uncertainty, we used the highest density recorded in reach three (46 redds, 12.7 redds/km, 1998) as the reach-scale response.

Channel slope

Several studies suggest an influence of channel slope or gradient on bull trout spawning (e.g. Fraley et al. 1981, Leathe and Enk 1985, Shepard 1985, Fraley and Shepard 1989). Montgomery et al. (1999) describe the correspondence between stream channel slope and channel morphology, as well as a strong association between channel slope and salmonid species presence/spawning distributions in three Pacific Northwest watersheds. We examined the possible influence of stream channel slope on bull trout spawning density at three scales: subbasin, total redd-surveyed length within subbasin and individual redd-survey reach. Average subbasin channel slope was calculated as the difference in elevation between the subbasin delineation pourpoint and the most upstream point of a routed GIS hydrography coverage, divided by the routed stream distance between the same two points. The routed hydrography corresponded very closely, though not perfectly, with perennial streams as mapped on USGS 7.5-minute topographic quad maps.

We calculated mean redd-surveyed channel slope for each subbasin as: (upper endpoint elevation of the uppermost reach surveyed for redds in any year, in meters) – (lower endpoint elevation of lowest reach surveyed in any year) / stream length (m) between the same endpoints. Delineated redd-survey reach breaks were obtained from unpublished Forest Service lists. Elevations were obtained from USGS 7.5-minute quads.

Some subbasins were nested within larger subbasins. For these cases we used whichever stream segment was surveyed to the greatest distance and elevation above the nested subbasin pourpoint (in or outside the nested subbasin) to determine average channel slope for the larger subbasin. For example, Little Stony Creek is nested within the Stony Creek subbasin. Little Stony was surveyed to a greater distance and elevation above its mouth (subbasin pourpoint) than was Stony Creek above Little Stony. Therefore, the upper endpoint in Little Stony was used to calculate average channel slope for both the Stony and Little Stony subbasins. Likewise, the upper survey reach endpoint in Copper Creek was used in channel slope calculations for Copper Creek, Copper above Green Canyon and Middle Fork above East Fork (within which Copper Creek is nested) subbasins.

We similarly calculated average slope for the single redd-survey reach within each subbasin that registered the highest reach-scale redd density in any survey year as the difference in elevation divided by the routed stream length between upper and lower survey-reach endpoints. A single exception was reach five of Copper Creek, which contained the highest recorded redd density in Copper Creek based on 4 redds in 1996 within a reach length of only 0.3 km. In the other three years it was surveyed, a single redd was found in this reach in 1994, none in 1997 and 1998. Thus, we judged the high 1996 density largely an artifact of the very short reach length. We therefore combined reaches five and six, using the resulting combined-reach redd density and reach slope for this analysis.

Stream temperature

Stream temperatures were monitored near the subbasin pourpoint in 14 of our 19 subbasins during summer-fall in both 1998 and 1999, although the individual subbasins monitored varied between years. Twelve of 19 subbasins were monitored both years. Sixteen of 19 were monitored at least one year. We used multiple-regression modeling from the same set of candidate predictor variables used in this report (excluding stream temperature) to develop a model predicting the maximum 7-consecutive-day average of daily maximum water temperatures ("maximum weekly maximum temperature", MWMT) for each subbasin. We chose this temperature metric for several reasons: 1) bull trout are a coldwater species believed to be limited both in range and in spawning habitat requirements by higher temperatures; 2) various maximum-temperature metrics (e.g. maximum daily maximum, maximum daily average, MWMT, maximum 7-day average of daily averages, etc.) are highly correlated (Hillman and Essig 1998, our unpublished data); 3) MWMT may better capture cumulative biological effects of a sustained warm period that may be of equal or greater importance than acute effects of instantaneous maximum temperature, while still capturing most of the influence of instantaneous maxima; and 4) MWMT has been used for temperature standards within the regulatory environment (EPA 1997, Hillman and Essig 1998).

To obtain MWMT values for subbasins where stream temperatures were not monitored, we developed multiple-regression models predicting MWMT from natural log average channel slope over 5 km above subbasin pourpoint, natural log stream length within subbasin and subbasin proportion in granitics. These variables explained 93.5% of the variation in 1999 MWMT ($p<0.0005$) and 88.4% of the variation in 1998 MWMT ($p<0.0005$). There were, however, significant correlations of log channel slope over 5 km with log stream length ($r= -.519$, $p<0.05$) and granitics proportion($r= -.652$, $p<0.01$). To maintain sample size, we used actual MWMT values along with predicted MWMT from these models for subbasins where temperatures were not monitored in a given year as our stream temperature metrics. For each analysis (unstratified and stratified samples, reach-scale and surveyed-length scale redd densities), we used whichever year's MWMT was more strongly correlated with redd densities as the candidate predictor.

Bounded alluvial valley segments (BAVS)

Numerous studies suggest the importance of groundwater influence to bull trout spawning habitat (e.g. Block 1955, Fraley et al. 1981, Shepard 1985, Fraley and Shepard 1989, Baxter 1997). In the Swan River basin, Montana, Baxter et al. (1999) found that bull trout redd counts and densities did not vary significantly with standard geomorphic metrics such as drainage area, stream order or stream gradient, but that redd counts were significantly and positively correlated with both the area and length of bounded alluvial valley segments (BAVS) accessible to spawners. BAVS, considered to be areas of extensive groundwater-surface water interaction, were defined as unconfined stream reaches at least 500 m long, bounded laterally by valley widths >50 m and longitudinally by valley constrictions and gradient steps >10%.

We applied this definition to quantify BAVS length, total number of constrictions/gradient steps ("knickpoints"), number of knickpoints below identified BAVS, BAVS proportion (BAVS length/stream length) and knickpoints-below-BAVS/stream length for each of our subbasin analysis units. We considered either valley constriction to <50m or a gradient step >10% as knickpoints. In the largest tributaries and major forks, we adjusted the valley constriction criterion upward to as wide as 100-200 m at several sites where we judged marked valley constriction at downstream limits of wide floodplain reaches likely to result in groundwater upwelling. Several of these were also predicted sites of groundwater upwelling based on similar rationale in an Ecological Classification of the Rock Creek drainage (Jensen 1998), further supporting the validity of this adjustment.

Brook trout presence

We used records in the Montana Rivers Information System (MRIS) database to determine brook trout presence. We considered brook trout present within an analysis unit (delineated subbasin) if there were any records of reported presence in stream reaches within that subbasin. Since MRIS compiles records from various sources over time, there are some concerns about reliability of these records. For example, the fish species presence records for the Ross Fork report brook trout "rare" from mouth to headwaters. However, the only specific Ross Fork population survey records (from 1993) reported brook trout present only in and below Moose Meadow Creek. In such cases, we chose to risk erring on the side of detecting an effect of brook trout presence where there might be none by considering brook trout present throughout the subbasin, on the basis of the "rare mouth to headwaters" report.

Geologic districts/granitics

The granitics category in a geologic district classification of the Rock Creek drainage (Jensen 1998) had some predictive power in exploratory analyses for both stream temperature and bull trout spawning use and captured nearly all the variability in the geologic district classification within the drainage. This classification, however, combined some minor rock types and small inclusions of granitics into adjacent classes. In an effort to increase resolution, we re-calculated areas of granitics within subbasins from the original rock type GIS coverage (Jensen 1998, derived from Ross et al. 1955) from which the geologic districts had been classified.

Aspect class

Subbasin aspect class was estimated by placing a straightedge on a map in a position best approximating the average stream valley axis within the subbasin of the main stream segment from pourpoint to headwaters. Deviation of this axis in degrees from a north-south axis was measured and located in one of ten 9°-wide arcs extending to either side from the N-S axis. This resulted in ten aspect classes with values ranging from one for an average stream axis deviating ≤9° either way from N-S orientation, to ten for an average stream axis deviating ≤9° from E-W orientation. Our assumption was that lower aspect classes would be less prone to shading during midday.

Wilderness/roadless proportion

Designated wilderness (NRIS 2001) and Forest Service Inventoried Roadless Areas (USDAFS 2001) were summarized by area for each subbasin analysis unit using the Tabulate Areas function in the Arcview Spatial Analyst extension. Wilderness and roadless coverages were visually examined in Arcview to confirm there was no detectable overlap between the two coverages. Wilderness and roadless areas within each subbasin were then summed under the assumption that any influences of wilderness or inventoried roadless status would be similar. The proportion of subbasin area consisting of wilderness/roadless (combined) area was also calculated for each subbasin.

Initial correlation analysis indicated wilderness/roadless area correlated strongly with measures of stream/subbasin "size" (subbasin total area, subbasin total routed stream length, stream order at pourpoint and stream order at maximum-redd-density reach; range of r: .700 to .899, all $p<0.01$). Therefore, only wilderness/roadless proportion of subbasin area was considered in further analyses. In addition to other analyses, scatterplots of wilderness/roadless proportion versus redd density were generated and examined for the unstratified sample and all strata, with redd densities at both scales. The difference in distributions of wilderness/roadless proportions between "low/none" (<2 redds/surveyed km) and "moderate/high" (≥2/km) redd-density subbasins in the unstratified sample was examined with boxplots and tested for significance using the nonparametric Mann-Whitney U test.

RESULTS

Surveyed-length-scale redd densities

Unstratified sample

Correlation analysis

Among all combinations of temperature metrics and scales at which channel and subbasin slopes and redd densities were examined for our 19 subbasins, redd densities generally correlated most strongly with channel slope, followed by stream temperature, subbasin relief, stream order, knickpoints-below-BAVS density and wilderness/roadless proportion (Table 2; Appendix A). Each of these measures correlated significantly with at least one of the four redd density metrics considered ($p<0.05$). Correlations of channel slope, subbasin relief, knicks-below-BAVS density and wilderness/roadless proportion with redd densities were consistently positive. Correlations of stream temperature and stream order with redd densities were consistently negative. Knicks-below-BAVS densities correlated significantly only with maximum redd density averaged over the total surveyed length within a subbasin ($p<0.05$). Positive correlation of wilderness/roadless proportion with redd density was significant only for a two-level classification of surveyed-length-scale redd densities into "low/none" (<2/km) and "moderate/high" (≥2/km) categories ($p<0.05$). Among the three channel-slope scales examined, maximum redd densities summarized over the total redd-surveyed stream length within a subbasin correlated most strongly with channel slope averaged over the same stream length (Table 2).

Within this subset of response and candidate predictor variables, positive correlations among the four redd density metrics were all highly significant ($p<0.01$; r range 0.813 to 0.938, Table 2). The 1998 and 1999 stream temperature metrics were strongly correlated with each other ($r=0.951$, $p<0.01$), and both showed strong negative correlations with all subbasin relief and channel slope metrics ($p<0.01$) (Table 2). Also, although not considered as a candidate predictor for spawning habitat modeling, channel slope averaged over 5 km above the subbasin pourpoint was the most significant predictor in the model used to obtain predicted stream temperature values for subbasins where temperatures were not monitored. Correlations of stream order with channel slope were negative and highly significant at all three scales ($p<0.01$). Correlation of stream order with temperature was positive and highly significant both years ($p<0.01$) (Table 2).

Multiple regression results, surveyed-length-scale response

When redd densities were calculated over the total redd-surveyed length within a subbasin in a given year, maximum values within the period of record (1993-2000) ranged from zero to 10.3 redds/surveyed km (Table 3). In four separate simple regression models meeting our model-fitting criteria, average redd-surveyed channel slope, maximum-redd-density-reach average channel slope and knickpoints-below-BAVS density were positively associated with redd densities, while 1999 maximum 7-day average of daily maximum temperatures ("Maximum Weekly Maximum Temperature, MWMT") was negatively associated with redd densities (Table 4). No multivariate regression models meeting our significance, collinearity and overfitting criteria were obtained with surveyed-length-scale redd densities.

Average redd-surveyed channel slope alone explained 50% of the variation in maximum redd density over the surveyed stream length ($p=0.001$). MWMT alone explained 37% of the variation ($p=0.006$), maximum-redd-density-reach average channel slope alone explained 30% ($p=0.016$) and knicks-below-BAVS density explained 25% ($p=0.030$) (Table 4).

Table 2. Correlations among redd densities and most-correlated environmental variables at several scales/resolutions.

	mxrrdord	slope46	lnbsnslp	lnsrvslp	lnmxrdsl	ln1kbBdn	wldrlppn	lnm7msg2	p7d98msg	mxrdddns	rddns3cl	rddns2cl	ln1mxrrd
pptorder	.874(**)	-0.360	-.597(**)	-.655(**)	-.664(**)	-0.153	-.482(*)	.692(**)	.612(**)	-.534(*)	-.590(**)	-.576(**)	-.483(*)
mxrrdord		-0.240	-0.444	-.496(*)	-.601(**)	-0.102	-0.452	.635(**)	.538(*)	-0.386	-.467(*)	-0.396	-0.418
slope46			.653(**)	.676(**)	.592(**)	0.137	0.151	-.616(**)	-.632(**)	.539(*)	.540(*)	.522(*)	.539(*)
lnbsnslp				.888(**)	.755(**)	0.217	0.094	-.767(**)	-.769(**)	.651(**)	.700(**)	.632(**)	.720(**)
lnsrvslp					.921(**)	0.246	0.131	-.874(**)	-.856(**)	.705(**)	.768(**)	.637(**)	.706(**)
lnmxrdsl						0.153	0.069	-.914(**)	-.871(**)	.543(*)	.564(*)	0.416	.538(*)
ln1kbBdn							0.353	-0.236	-0.195	.499(*)	0.435	0.324	0.318
wldrlppn								-0.186	-0.142	0.296	0.395	.561(*)	0.244
lnm7msg2									.951(**)	-.607(**)	-.619(**)	-.513(*)	-.591(**)
p7d98msg										-.575(*)	-.577(**)	-.522(*)	-.637(**)
mxrdddns											.938(**)	.813(**)	.902(**)
rddns3cl												.884(**)	.895(**)
rddns2cl													.851(**)

*correlation is significant at $\alpha = 0.05$
**correlation is significant at $\alpha = 0.01$

key:

pptorder	stream order at subbasin delineation pourpoint
mxrrdord	stream order at maximum-single-reach-redd-density reach
slope46	proportion subbasin area in slope classes >46% (subbasin relief/"ruggedness")
lnbsnslp	natural log average subbasin channel slope
lnsrvslp	natural log average redd-surveyed channel slope
lnmxrdsl	natural log average channel slope over maximum-single-reach-redd-density reach
ln1kbBdn	natural log (1+(knicks below BAVS/stream length))
wldrlppn	proportionn subbasin area wilderness/inventoried roadless NF
lnm7msg2	natural log ('99 MWMT) + model-predicted for missing
p7d98msg	'98 MWMT + model-predicted for missing
mxrdddns	maximum recorded density, redds/km over total surveyed length in subbasn
rddns3cl	redd density, 3 classes (<2/km, 2-5.9/km, ≥6/km)
rddns2cl	redd density, 2 classes (<2/km, ≥2/km)
ln1mxrrd	natural log (1+single-survey-reach maximum redd density)

Table 3. Maximum recorded redd densities in 19 Rock Cr. drainage subbasins, summarized at total-surveyed-length and single-survey-reach scales.

subbasin (number of survey years)	number of redds in max-density year (year)	total surveyed stream length in max-density year, km	**maximum redds/km total surveyed stream length in subbasin**	number of redds in maximum-density single survey reach (year)	maximum-density-single-survey-reach length, km	**maximum single-survey-reach redds/km**
Gilbert Cr. (3)	6 (97)	3.4	**1. 8**	6 (97)	3.4	**1.8**
Ranch Cr. (5)	29 (99)	10.4	**2.8**	19 (99)	4.8	**3.9**
Welcome Cr. (5)	25 (97)	3.6	**6.9**	25 (97)	3.6	**6.9**
Alder Cr. (3)	41 (96)	6.0	**6.8**	35 (96)	2.4	**14.5**
Hogback Cr. (3)	14 (99)	2.8	**5.0**	14 (99)	2.8	**5.0**
Stony Cr. (8)	54 (98)	6.8	**8.0**	46 (98)	3.6	**12.7**
Little Stony Cr. (3)	29 (98)	4.8	**6.0**	10 (00)	1.1	**8.9**
West Fork Rock Cr. (4)	4 (93/7)	9.5	**0.4**	4 (93/7)	9.5	**0.4**
Ross Fork blw Falls Cr. (3)	0 (96/7/9)	15.0	**0.0**	0 (96/7/9)	5.0	**0.0**
Ross Fork abv Falls Cr. (4)	20 (98)	6.0	**3.3**	20 (98)	6.0	**3.3**
Sand Basin Cr. (1)	1 (99)	7.2	**0.1**	1 (99)	0.7	**1.4**
Bowles Cr. (2)	0 (96/9)	2.3	**0.0**	0 (96/9)	1.2	**0.0**
Middle Fork blw Copper (3)	1 (93)	8.4	**0.1**	1 (93)	8.4	**0.1**
Middle Fork abv Copper (8)	47 (98)	12.4	**3.8**	28 (97)	2.9	**9.7**
Meadow Cr. (4)	4 (98)	2.4	**1.7**	5 (99)	2.7	**1.8**
Copper blw Grn Cnyn (8)	25 (98)	4.7	**5.4**	25 (98)	4.7	**5.4**
Copper abv Grn Cnyn (6)	6 (96)	6.1	**1.0**	5 (96)	2.4	**2.1**
Meyers Cr. (4)	10(97/8/0)	3.2	**3.1**	10(97/8/0)	3.2	**3.1**
Carpp Cr. (8)	62 (98)	6.0	**10.3**	41 (98)	3.6	**11.3**

Table 4. Most-significant multiple regression models predicting maximum bull trout redds/surveyed stream length within 19 Rock Creek drainage subbasins.

			predictors	coefficient	std. error	t	p
Model 1	**R^2**	**.497**	**intercept**	**17.331**	**3.412**	**5.079**	**<0.0005**
	Adj. R^2	**.468**					
	F	**16.827**					
	p	**0.001**	**natural log average redd-surveyed channel slope**	**3.787**	**.923**	**4.102**	**0.001**
	df	**18**					
Model 2	**R^2**	**.368**	**intercept**	**26.058**	**7.192**	**3.623**	**0.002**
	Adj. R^2	**.331**					
	F	**9.906**	**natural log '99 MWMT (+model-predicted for missing)**	**-8.618**	**2.738**	**-3.147**	**0.006**
	p	**0.006**					
	df	**18**					
Model 3	R^2	.295	intercept	14.259	4.086	3.490	0.003
	Adj. R^2	.253					
	F	7.009	natural log maximum-redd-density-reach average channel slope	2.822	1.059	2.664	0.016
	p	0.016					
	df	18					
Model 4	R^2	.249	intercept	.884	1.267	.698	0.495
	Adj. R^2	.205					
	F	5.640	natural log (1+(knickpoints-below-BAVS/km))	18.597	7.830	2.375	0.030
	p	0.030					
	df	18					

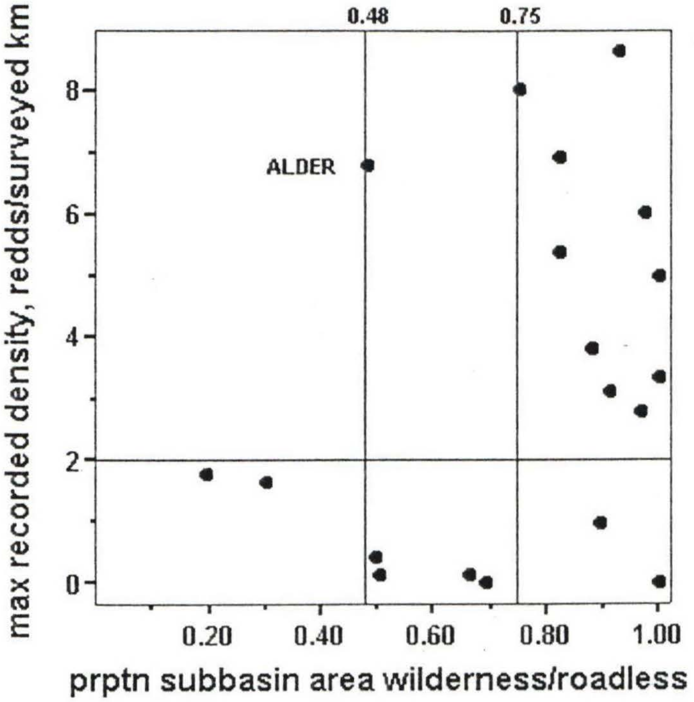
Bold denotes model and all predictor coefficients' $p < 0.01$.

Wilderness/roadless proportion

No regression models were found that met our selection criteria and included wilderness/roadless proportion as a predictor of redd densities (regression models were examined only for the two continuous redd-density metrics). This, in combination with lack of significant correlation between wilderness/roadless proportion and the continuous redd-density metrics, indicates that any positive association of wilderness/roadless proportion with redd densities in the Rock Creek drainage is not strongly linear.

Examination of scatterplots and boxplots, in conjunction with the two-level redd-density classification, however, suggested a possible threshold function relating wilderness/roadless proportion to redd densities (Figure 3). Maximum redd densities >2/km occurred only in subbasins with >48% of their areas within designated wilderness or inventoried roadless national forest. Except for Alder Creek, all higher-redd-density subbasins had wilderness/roadless proportions >.75.

Figure 3. **Maximum surveyed-length-scale redd densities in relation to proportion of area in designated wilderness/inventoried roadless national forest in 19 Rock Creek subbasins.**



Since samples after stratification were subsets of the data shown in Figure 3, and since results were similar for redd densities summarized at both scales, this generalization held for all stratifications as well, although the suggested relationship appeared somewhat stronger (e.g. Figure 4) or weaker (e.g. Figure 5) depending on which particular cases were included in a stratum and the scale at which redd densities were summarized.

Figure 4. Maximum single-survey-reach-scale redd densities in relation to proportion subbasin area in designated wilderness/inventoried roadless national forest in 10 higher-granitics Rock Creek subbasins.

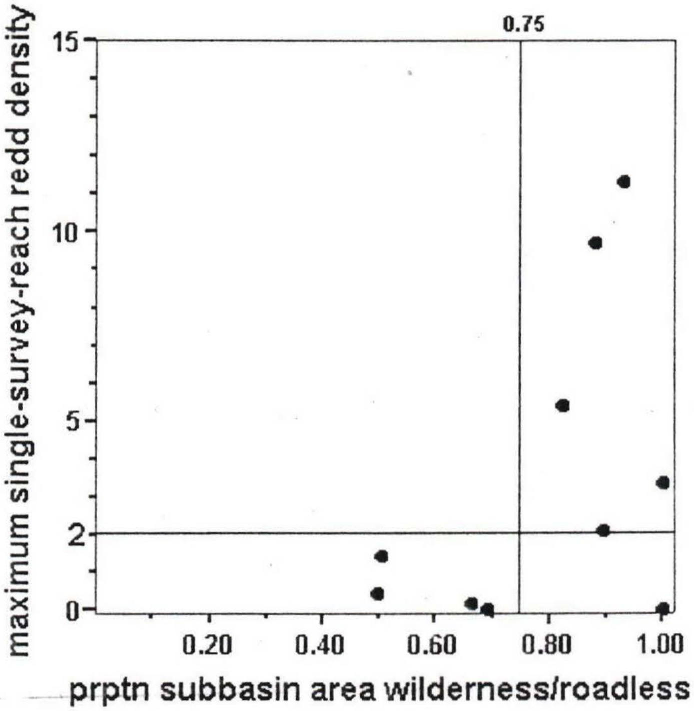
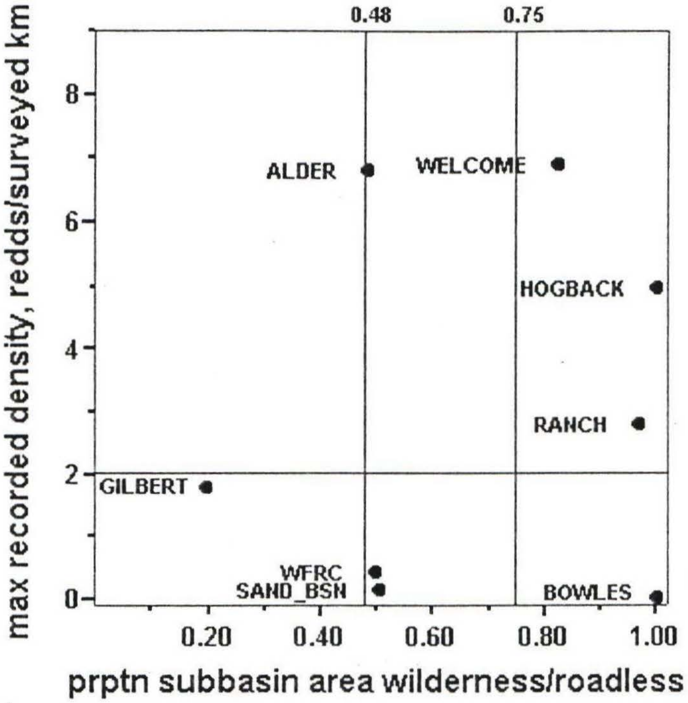
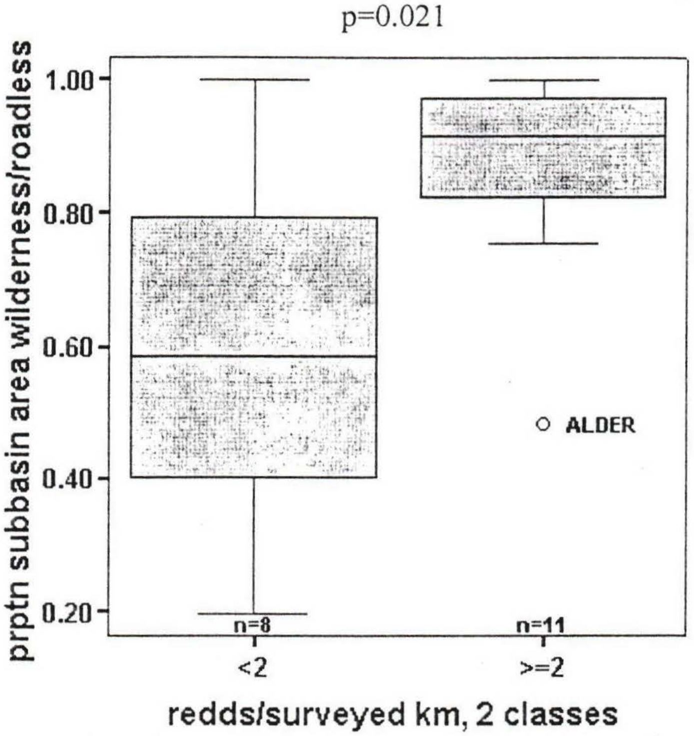


Figure 5. Maximum surveyed-length-scale redd densities in relation to proportion subbasin area in designated wilderness/inventoried roadless national forest in 8 Rock Creek subbasins with fluvial dominant geomorphology.



Distribution of wilderness/roadless proportions was significantly higher in the higher-redd-density group (Figure 6) (p=0.021, one-tailed Mann-Whitney U test, not corrected for ties). Correlation of wilderness/roadless proportion with road densities was strongly negative, as expected (r= -.922, p<0.01).

Figure 6. Two-level redd density classification in relation to proportion subbasin area in designated wilderness or inventoried roadless national forest in 19 Rock Creek subbasins.



Alder Creek, the outlier to a .75 wilderness/roadless proportion threshold, has something of a split personality. Roads related to pre-1991 timber harvest are confined to roughly half the subbasin north of Alder's tributary Lavina Creek and of the Alder mainstem below Lavina. From Lavina Creek and the lower Alder mainstem south, including the majority of the main branch and all of Alder's longest (unnamed) tributary, the subbasin consists of contiguous inventoried roadless national forest.

Stratified samples

Stratification by average subbasin channel slope

Lower-gradient (<5%) stratum (n=10 subbasins)

Surveyed-length-scale response

After stratification by average subbasin channel slope, subbasin channel slope remained the only candidate predictor within the lower-gradient stratum that was significantly correlated with maximum redd densities averaged over the total redd-surveyed length in each subbasin (r=.674, p<0.05). Among candidate predictors within the stratum, correlation of average subbasin channel slope was negative with combined road-trail density (-.769, p<0.01), proportion in seedling/sapling class (-.761, p<0.05) and road density (-.750, p<0.05); and positive with proportion at elevation above 7000 feet (.716, p<0.05), proportion with precipitation >32 inches (.686, p<0.05) and proportion with slope >46% (.638, p<0.05). Maximum redd densities within this stratum ranged only up to 5.36/km and only two cases exceeded 4/km (i.e. most higher-redd-density subbasins were in the higher-gradient stratum). Average subbasin channel slope alone explained 45% of the variation in redd density within the lower-gradient stratum (p=0.033) (Table 5). No other models meeting our significance, collinearity and overfitting criteria were found.

Table 5. Most-significant regression model predicting maximum bull trout redds/surveyed stream length in lower-gradient (<5%) stratum of average subbasin channel slopes (n=10).

			Predictor variables	coefficient	std. error	t	p
Model 5	R^2	.454	intercept	15.055	5.127	2.936	0.019
	Adj. R^2	.386					
	F	6.648	natural log average subbasin channel slope	3.608	1.399	2.578	0.033
	p	0.033					
	df	9					

Bold denotes model and all predictor coefficients' p < 0.01.

Stratification by average subbasin channel slope

Higher-gradient (≥5%) stratum (n=9 subbasins)

Surveyed-length-scale response

In contrast with the lower-gradient stratum, average subbasin channel slope did not correlate significantly with redd density within this stratum (r=.108, p=0.782), indicating higher subbasin-scale average gradient was associated with higher redd density within the lower range of channel slopes in our sample, but not within the upper range. Stream length within bounded alluvial valley segments (BAVS) (r=.828, p=0.006) and trail density (r=.698, p=0.036) correlated positively with surveyed-length-scale redd densities in this stratum. Correlation of BAVS length with granitics proportion was strong within this stratum (r=.832, p<.01), while they were virtually uncorrelated in the unstratified sample (r= -.055). BAVS length also correlated positively with proportion in precipitation classes >32 inches (r=.772, p<0.05) and trail density (r=.687, p<0.05) and negatively with distance to nearest known bull trout spawning tributary (r= -.690, p<0.05).

In the most significant models we obtained for higher-gradient subbasins, redd densities increased with BAVS length, channel slope and trail density (Table 6). BAVS length alone explained 69% of the variation in surveyed-length-scale redd densities in this stratum (p=0.006); trail density alone explained 49% (p=0.036). BAVS length in combination with average redd-surveyed channel slope explained 85% of the variation (p=0.003). Influence statistics flagged Welcome Creek as possibly influential in this model (Figure 7).

Figure 7. Model 8. Maximum surveyed-length-scale redd densities (vertical axis) in relation to stream length within BAVS and average redd-surveyed channel slope in higher-gradient stratum of average subbasin channel slope (untransformed variables shown).

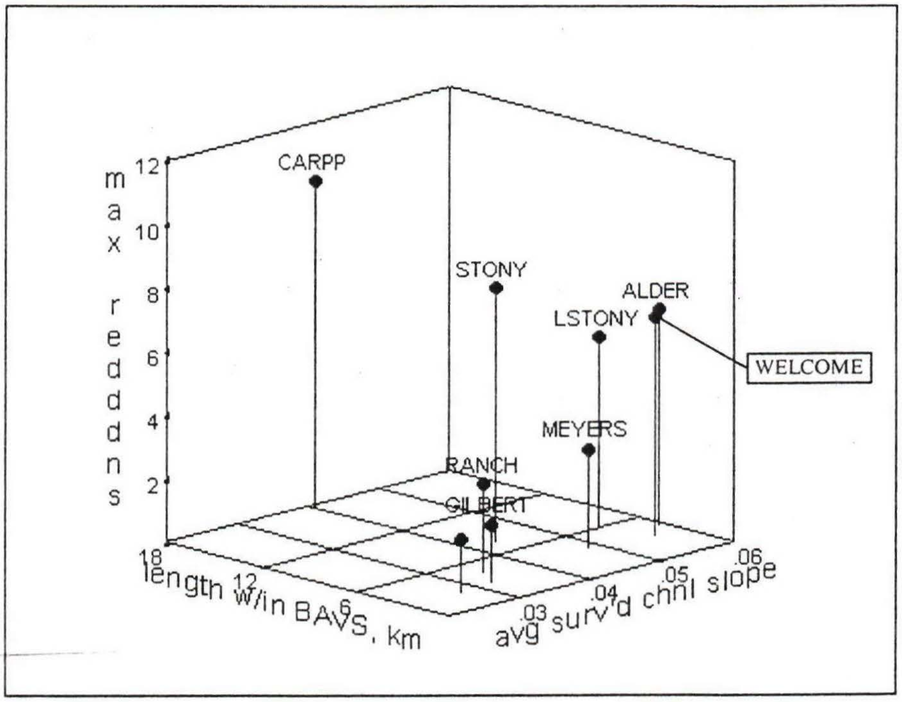


Table 6. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in higher-gradient (≥5%) stratum of average subbasin channel slopes (n=9).

			Predictor variables	coefficient	std. error	t	p
Model 6	**R^2**	**.685**	**intercept**	**-3.259**	**2.263**	**-1.440**	**0.193**
	Adj. R^2	**.640**					
	F	**15.252**	**natural log (1+stream km w/in BAVS in subbasin)**	**4.837**	**1.239**	**3.905**	**0.006**
	p	**0.006**					
	df	**8**					
Model 7	R^2	.488	intercept	2.879	1.203	2.393	0.048
	Adj. R^2	.415					
	F	6.666					
	p	0.036	natural log (1+(trail density, km/km^2))	10.397	4.027	2.582	0.036
	df	8					
Model 8	R^2	.852	intercept	12.292	6.232	1.972	0.096
	Adj. R^2	.802	natural log (1+stream km w/in BAVS in subbasin)	4.338	.939	4.620	0.004
	F	17.206					
	p	0.003	natural log average redd-surveyed channel slope	4.638	1.790	2.591	0.041
	df	8					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Stratification by average redd-surveyed channel slope

Lower-gradient (<3%) stratum (n=10 subbasins)

Surveyed-length-scale response

Higher average subbasin elevations were associated with higher redd densities in the lower-gradient (<3%) stratum of channel slopes averaged over the total redd-surveyed stream length in each subbasin. Only average subbasin elevation correlated significantly with redd densities summarized over the redd-surveyed stream length in this stratum (r=.678, p<0.05). Average subbasin elevation also correlated significantly with average subbasin channel slope (.751, p<0.05) and subbasin proportion in solar radiation classes >300 W/m^2 (.676, p<0.05). Average subbasin elevation alone accounted for 46% of the redd density variation (p=0.031) (Table 7). No other models meeting our significance, collinearity and overfitting criteria were found with surveyed-length-scale redd densities in this stratum.

Table 7. Most-significant regression model predicting maximum bull trout redds/surveyed stream length in lower-gradient (<3%) stratum of average surveyed channel slopes (n=10).

			Predictor variables	coefficient	std. error	t	p
Model 9	R^2	.459	intercept	-33.295	13.386	-2.487	0.038
	Adj. R^2	.392					
	F	6.796					
	p	0.031	average subbasin elevation, feet	.004895	.002	2.607	0.031
	df	9					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Stratification by average redd-surveyed channel slope
Higher-gradient (≥3%) stratum (n=9 subbasins)
Surveyed-length-scale response

Surveyed-length-scale redd densities were positively correlated with stream length within BAVS ($r=.756$, $p<0.05$) and trail densities (.678, $p<0.05$) in higher-gradient streams. Among candidate predictors, BAVS length correlated positively with granitics proportion (.826, $p<0.01$), knicks-below-BAVS density (.750, $p<0.05$) and average subbasin elevation (.745, $p<0.05$); trail densities correlated positively with granitics proportion (.753, $p<0.05$).

BAVS length alone accounted for 57% of the redd-density variation in higher-gradient streams ($p=0.018$) (Table 8). Trail density alone explained 46% of the variation ($p=0.045$). No other models meeting our criteria were found in this stratum.

Table 8. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in higher-gradient (≥3%) stratum of average surveyed channel slopes (n=10).

			Predictor variables	coefficient	std. error	t	p
Model 10	R^2	.572	intercept	-1.260	2.340	-.538	0.607
	Adj. R^2	.511					
	F	9.346	natural log (1+stream km w/in BAVS in subbasin)	3.923	1.283	3.057	0.018
	p	0.018					
	df	8					
Model 11	R^2	.460	intercept	3.340	1.178	2.835	0.025
	Adj. R^2	.383					
	F	5.960					
	p	0.045	natural log (1+trail density, km/km^2)	9.364	3.835	2.441	0.045
	df	8					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Temperature Stratification
1999 MWMT (+ model-predicted for missing) <13.3°C (n=9)
Surveyed-length-scale response

A 1999 MWMT cutpoint of 13.3°C created cool (n=9) and warm (n=10) strata identical to those from a 1998 MWMT cutpoint of 13.0°C. Trail density (.788, $p<0.05$), BAVS length (.762, $p<0.05$), granitics proportion (.720, $p<0.05$) and knicks-below-BAVS density (.688, $p<0.05$) correlated positively with surveyed-length-scale redd densities in cooler streams, while correlations of redd densities with stream order at subbasin pourpoint ($r= -.745$, $p<0.05$) and brook trout presence (-.703, $p<0.05$) were negative. Among candidate predictors, trail density correlated positively with granitics proportion (.751, $p<0.05$) and BAVS length (.706, $p<0.05$). BAVS length correlations were positive with granitics proportion (.893, $p<0.01$) and knickpoints-below-BAVS/stream km (.778, $p<0.05$). Stream order at pourpoint correlated positively with 1999 MWMT (.882, $p<0.01$), brook trout presence (.791, $p<0.05$) and distance to nearest known bull trout spawning tributary (.721, $p<0.05$), and negatively with redd-surveyed channel slope (-.810, $p<0.01$). Granitics proportion correlated positively with knicks-below-BAVS density (.675, $p<0.05$). Correlation of brook trout presence with average redd-surveyed channel slope was strongly negative (-.869, $p<0.01$). Knicks-below-BAVS density correlated positively with proportion in precipitation classes >32 inches (.767, $p<0.05$) and negatively with distance to nearest known bull trout spawning tributary (-.698, $p<0.05$).

Each candidate predictor that was significantly correlated with redd density produced a significant simple regression model explaining from 47% to 62% of the redd-density variation (R^2 range .473 to .622; model p range 0.041 to 0.012; Table 9). Trail density, BAVS length and knicks-below-BAVS density were positively associated with redd densities, while associations of stream order and brook trout presence with redd density were negative.

A multiple regression model with stream order and trail density as predictors accounted for 91% ($p=0.001$) of the variation in surveyed-length-scale redd densities in cooler streams (Table 9). Influence statistics suggest Carpp Creek may be influential in this model (Figure 8).

A model with trail densities and brook trout presence as predictors accounted for 87% of redd-density variation ($p=0.002$). Influence statistics flagged Hogback, Meyers and Ranch Creeks as possibly influential in this model (Figure 9).

Trail density and redd-surveyed channel slope combined to account for 83% of redd-density variation ($p=0.005$). Influence statistics suggest Alder & Carpp Creeks may be influential in this model (Figure 10).

Trail density combined with stream temperature ('99 MWMT) to explain 87% of redd-density variation ($p=0.002$). Influence statistics suggest Carpp and Meyers Creeks may be influential in this model (Figure 11).

A model with BAVS length and stream order as predictors accounted for 83% of redd-density variation ($p=0.005$). Analysis again suggested possible influence of Carpp and Meyers Creeks in the relationship (Figure 12).

Figure 8. Model 17. Maximum surveyed-length-scale redd densities (vertical axis) in relation to stream order and trail density in cooler stratum of '99 MWMT (untransformed variables shown).

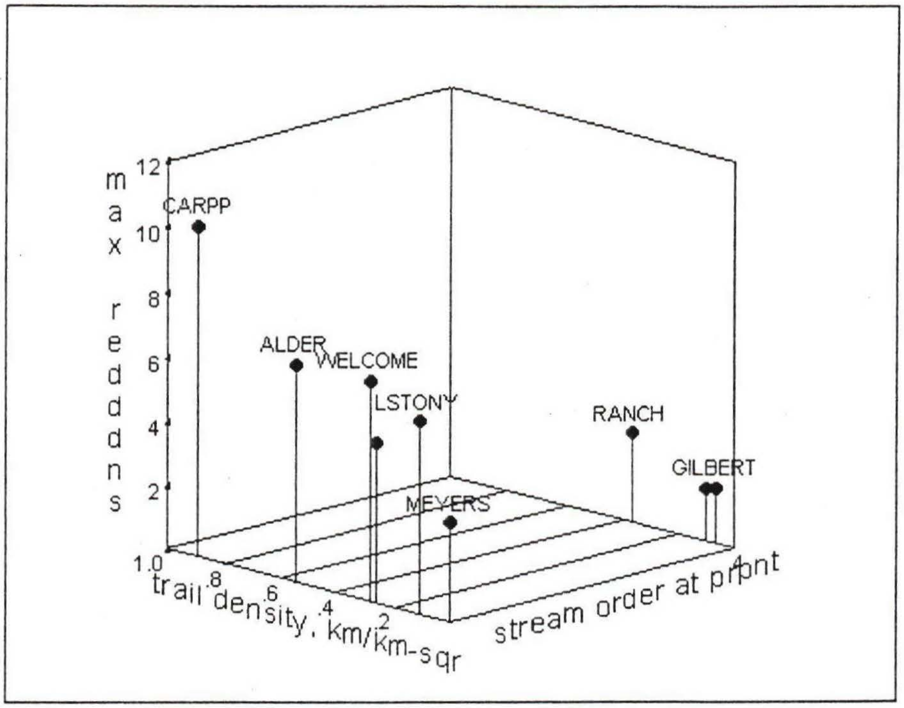


Figure 9. Model 18. Maximum surveyed-length-scale redd densities (vertical axis) in relation to trail density and brook trout presence in cooler stratum of '99 MWMT (untransformed variables shown).

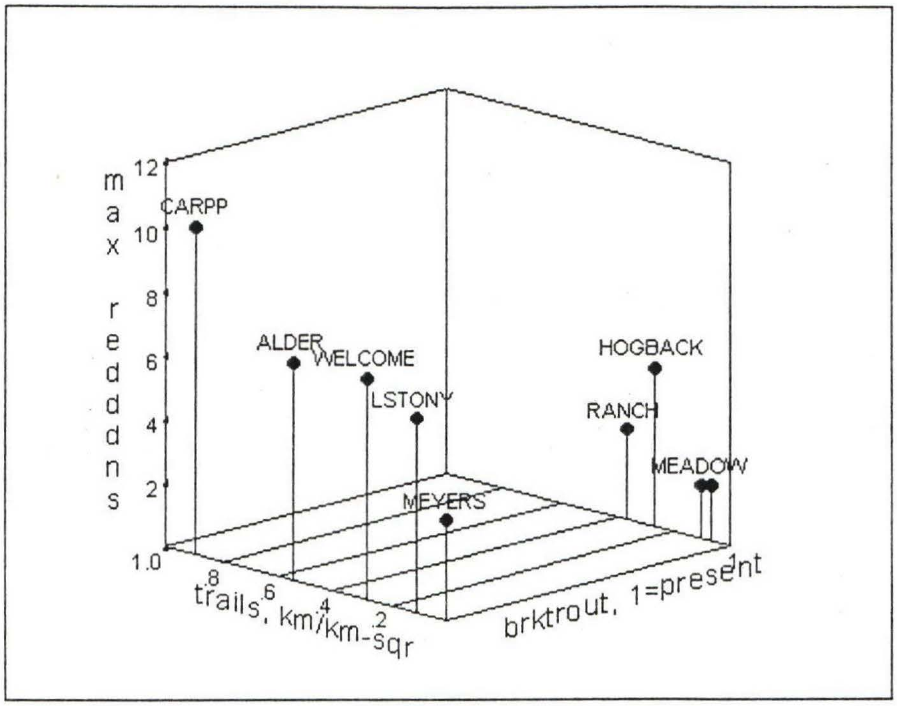


Figure 10. Model 19. Maximum surveyed-length-scale redd densities (vertical axis) in relation to trail density and average redd-surveyed channel slope in cooler stratum of '99 MWMT (untransformed variables shown).

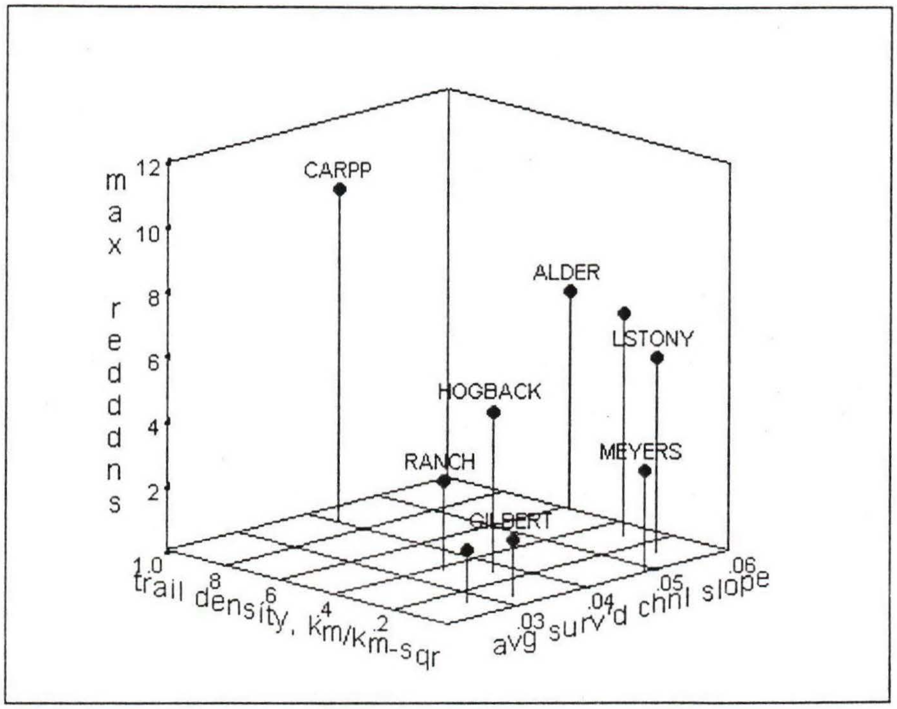


Figure 11. Model 20. Maximum surveyed-length-scale redd densities (vertical axis) in relation to trail density and stream temperature in cooler stratum of '99 MWMT (untransformed variables shown).

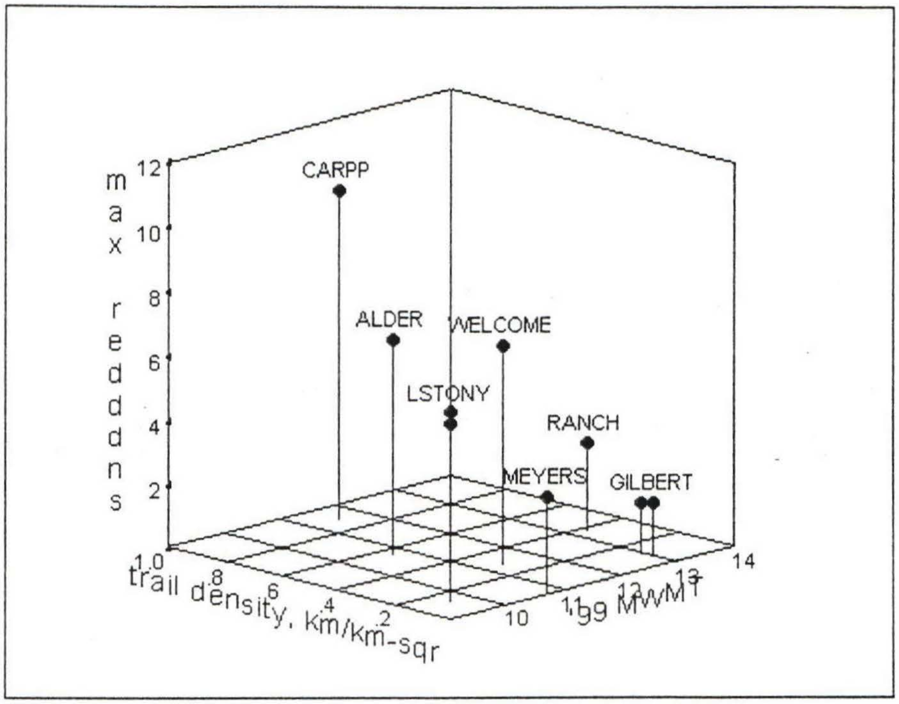


Figure 12. Model 21. Maximum surveyed-length-scale redd densities (vertical axis) in relation to BAVS length and stream order in cooler stratum of '99 MWMT (untransformed variables shown).

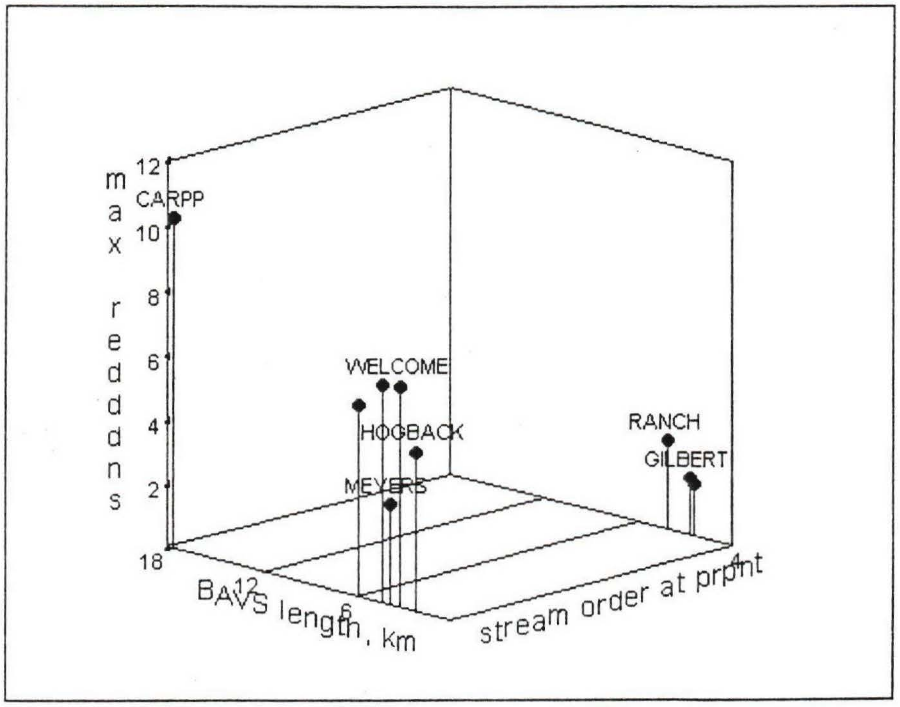


Table 9. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in cool (<13.3°C) stratum of 1999 MWMT (n=9).

			Predictor variables	coefficient	std. error	t	p
Model 12	R^2	.622	intercept	2.294	.996	2.304	0.055
	Adj. R^2	.568					
	F	11.505					
	p	0.012	natural log (1+trail density, km/km^2)	11.118	3.278	3.392	0.012
	df	8					
Model 13	R^2	.581	intercept	-1.843	2.268	-.813	0.443
	Adj. R^2	.521					
	F	9.712					
	p	0.017	natural log (1+stream km in BAVS w/in subbasin)	4.090	1.313	3.116	0.017
	df	8					
Model 14	R^2	.556	intercept	19.130	4.851	3.943	0.006
	Adj. R^2	.492					
	F	8.753					
	p	0.021	stream order at subbasin pourpoint	-4.263	1.441	-2.959	0.021
	df	8					
Model 15	R^2	.494	intercept	6.614	.972	6.801	<0.0005
	Adj. R^2	.422					
	F	6.837					
	p	0.035	brook trout, 1=reported presence	-3.814	1.459	-2.615	0.035
	df	8					
Model 16	R^2	.473	intercept	1.793	1.450	1.237	0.256
	Adj. R^2	.398					
	F	6.285					
	p	0.041	natural log (1+(knickpoints-below-BAVS/stream km))	20.536	8.191	2.507	0.041
	df	8					

Table 9 (continued)

			Predictor variables	coefficient	std. error	t	p
Model 17	**R^2**	**.909**	**intercept**	**13.549**	**2.633**	**5.147**	**0.002**
	Adj. R^2	**.879**	**natural log (1+(trail density, km/km^2))**	**8.778**	**1.814**	**4.839**	**0.003**
	F	**30.095**					
	p	**0.001**	**stream order at subbasin pourpoint**	**-3.211**	**.736**	**-4.363**	**0.005**
	df	**8**					
Model 18	R^2	.872	intercept	4.043	.807	5.013	0.002
	Adj. R^2	.830	natural log (1+(trail density, km/km^2))	9.039	2.145	4.215	0.006
	F	20.486					
	p	0.002	brook trout, 1=reported presence	-2.831	.825	-3.431	0.014
	df	8					
Model 19	R^2	.828	intercept	17.751	5.818	3.051	0.022
	Adj. R^2	.770	natural log (1+(trail density, km/km^2))	9.953	2.429	4.097	0.006
	F	14.406					
	p	0.005	natural log average redd-surveyed channel slope	4.774	1.783	2.677	0.037
	df	8					
Model 20	R^2	.873	intercept	33.460	9.059	3.694	0.010
	Adj. R^2	.831	natural log (1+(trail density, km/km^2))	11.130	2.050	5.429	0.002
	F	20.651					
	p	0.002	natural log '99 MWMT (+model-predicted for missing)	-12.815	3.716	-3.449	0.014
	df	8					
Model 21	R^2	.830	intercept	10.153	4.342	2.338	0.058
	Adj. R^2	.773	natural log (1+(stream km in BAVS w/in subbasin))	3.024	.973	3.109	0.021
	F	14.627					
	p	0.005	stream order at subbasin pourpoint	-3.070	1.037	-2.961	0.025
	df	8					

Bold denotes model and all predictor coefficients' $p < 0.01$

Temperature Stratification

1999 MWMT (+ model-predicted for missing) ≥ 13.3°C (n=9)

Surveyed-length-scale response

Within the warmer stratum of stream temperatures, surveyed-length-scale redd densities were positively correlated with average subbasin channel slope ($r=.740$, $p<0.05$) and proportion of subbasin area in slope classes >46% (.700, $p<0.05$), which, as predictors in simple regression models, explained 55% ($p=0.014$) and 49% ($p=0.024$), respectively, of the redd-density variation. However, correlation between these two candidate predictors was strong (.855, $p<0.01$). Subbasin channel slope also correlated negatively with combined road-trail density (-.760, $p<0.05$) and positively with alpine-glaciated-dominant geomorphology (.728, $p<0.05$). Proportion with slope >46% was positively correlated with dominant geomorphology within this stratum (.666, $p<0.05$).

A model combining average subbasin channel slope and seedling/sapling proportion explained 76% of redd-density variation in the stratum ($p=0.007$), again appearing to suggest a positive effect of seedling/sapling proportion on redd densities (Table 10). Seedling/sapling proportion (coefficient $p=0.042$) marginally met our criterion of predictor significance ($p<0.05$) for model inclusion, and its significance appeared largely driven by moderately-high seedling/sapling proportions combined with the highest redd densities in the stratum in Stony and Copper Creeks accounting for some of the variation remaining unexplained by subbasin channel slope. Influence statistics suggest the West Fork (WFRC) and Sand Basin Creek may be influential in this model (Figure 13). The model and both predictor coefficients remain significant if either WFRC alone ($R^2=.803$, $p=0.008$, $n=9$) or Sand Basin alone ($R^2=.815$, $p=0.006$, $n=9$) is excluded. If both are excluded, the model remains significant ($R^2=.808$, $p=0.016$, $n=8$), but seedling-sapling proportion loses significance as a predictor ($p=0.072$).

Figure 13. Model 24. Maximum surveyed-length-scale redd densities (vertical axis) in relation to average subbasin channel slope and seedling/sapling proportion in the warmer stratum of stream temperatures (untransformed variables shown).

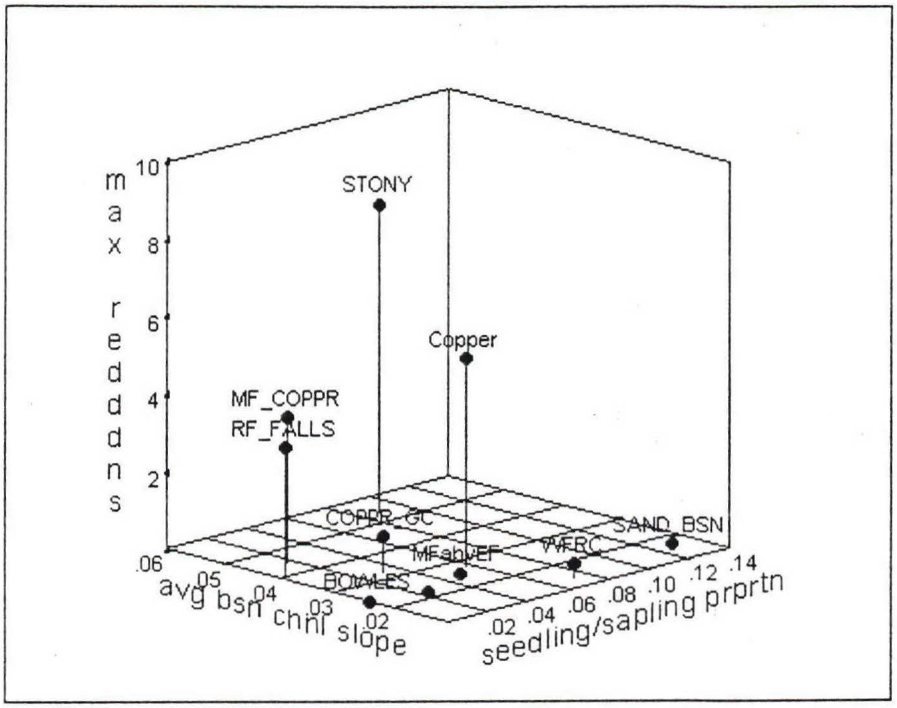


Table 10. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in warmer (≥13.3°C) stratum of 1999 MWMT (n=10).

			Predictor variables	coefficient	std. error	t	p
Model 22	R^2	.548	intercept	18.812	5.371	3.503	0.008
	Adj. R^2	.491					
	F	9.686					
	p	0.014	natural log average subbasin channel slope	4.592	1.475	3.112	0.014
	df	9					
Model 23	R^2	.490	intercept	-.0160	1.046	-.015	0.988
	Adj. R^2	.426					
	F	7.688					
	p	0.024	proportion subbasin area in slope classes >46%	23.703	8.548	2.773	0.024
	df	9					
Model 24	R^2	.760	intercept	21.517	4.319	4.982	0.002
	Adj. R^2	.692	natural log average subbasin channel slope	5.789	1.245	4.650	0.002
	F	11.097					
	p	0.007	natural log (1+proportion in seedling/sapling class)	3.075	14.883	2.491	0.042
	df	9					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Stratification by dominant geomorphology

Fluvial-dominant stratum (proportion in fluvial-dominant geomorphic class > .9; n=8)

Surveyed-length-scale response

In the eight subbasins shaped primarily by fluvial processes, correlations of surveyed-length-scale redd densities were positive with average redd-surveyed channel slope (r=.919, p<0.01) and negative with 1999 MWMT (-.841, p<0.01). Positive correlation of maximum-redd-density-reach average channel slope with redd densities was also highly significant (.892, p<0.01), but the reach-scale channel slope correlated strongly with surveyed-length-scale channel slope (.976, p<0.01). This probably reflects the fact that the maximum-redd-density reach was the total redd-surveyed length in four of the eight subbasins in the stratum. Subbasin proportion in solar radiation classes >300 W/m^2 correlated negatively with redd densities (-.736, p<0.05). Among candidate predictors, surveyed channel slope correlated significantly with seven of the ten other candidates (|r| range .912 to .750, all p<0.05). Correlations of surveyed channel slope with two other candidates had |r|>.6. Knickpoints below BAVS/km was the candidate predictor least correlated with both redd density (.423, not significant [ns]) and surveyed channel slope (.487, ns).

Higher surveyed-length-scale redd densities were associated with steeper channel slopes, lower stream temperatures, less solar radiation and lower stream order in subbasins where fluvial geomorphology dominated. Surveyed channel slope, 1999 MWMT and solar radiation each yielded a significant simple regression model explaining 85% (p=0.001), 71% (p=0.009) and 54% (p=0.037), respectively, of redd-density variation (Table 11). A model combining stream order at subbasin pourpoint and proportion of subbasin with solar radiation >300 W/m^2 accounted for 80% of redd-density variation in fluvial-dominant subbasins (p=0.017) (Figure 14). Close comparison of the solar radiation class GIS coverage with drainage topography suggests solar radiation may be functioning as a surrogate for local elevation at a finer resolution than the basin-scale elevation metrics we considered. Negative correlations with surveyed-length-scale redd densities of elevation at subbasin pourpoint, average subbasin elevation and proportion of subbasin at elevations >7000 feet (-.631, -.432 and -.594, respectively) were not significant, and a model combining pourpoint elevation and pourpoint order as predictors of redd densities was not significant. The three lowest redd densities and highest solar radiation values in this sample are from the only three subbasins in the upper Rock Creek drainage (West Fork Rock Creek and its nested tributary subbasins, Bowles and Sand Basin Creeks) (Figure 14), which also have the three highest values in the stratum for both pourpoint elevation and average elevation, further suggesting that solar radiation significance may largely capture a more localized elevation effect than we examined. Influence statistics suggest these same three subbasins may be influential in the model.

Figure 14. Model 28. Maximum surveyed-length-scale redd densities (vertical axis) in relation to proportion with solar radiation >300 W/m^2 and stream order at subbasin pourpoint in fluvial-dominant stratum of dominant geomorphology stratification.

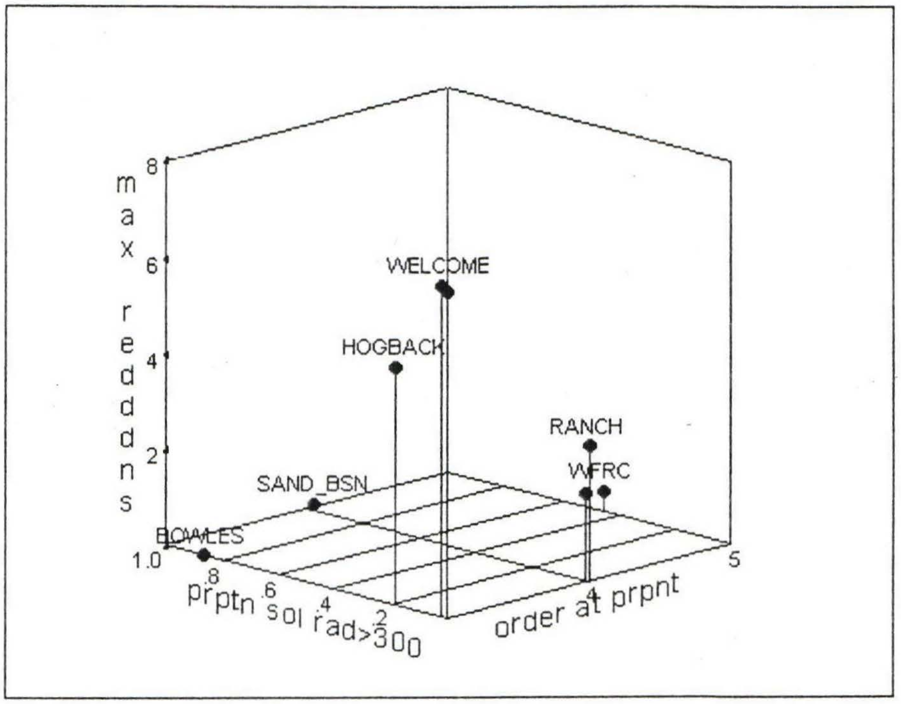


Table 11. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in fluvial-dominant stratum of dominant geomorphology stratification (n=8).

			Predictor variables	coefficient	std. error	t	p
Model 25	**R^2**	**.845**	**intercept**	**18.899**	**2.814**	**6.717**	**0.001**
	Adj. R^2	**.820**					
	F	**32.819**					
	p	**0.001**	**natural log average redd-surveyed channel slope**	**4.480**	**.782**	**5.729**	**0.001**
	df	**7**					
Model 26	**R^2**	**.707**	**intercept**	**34.598**	**8.342**	**4.148**	**0.006**
	Adj. R^2	**.658**					
	F	**14.446**					
	p	**0.009**	**natural log '99 MWMT (+ model-predicted for missing)**	**-12.298**	**3.235**	**-3.801**	**0.009**
	df	**7**					
Model 27	R^2	.542	intercept	4.621	.971	4.758	0.003
	Adj. R^2	.466					
	F	7.101					
	p	0.037	proportion subbasin in solar radiation classes > 300 W/m^2	-5.266	1.976	-2.665	0.037
	df	7					
Model 28	R^2	.803	intercept	11.752	2.851	4.122	0.009
	Adj. R^2	.725	proportion subbasin in solar radiation classes > 300 W/m^2	-4.704	1.435	-3.279	0.022
	F	10.222					
	p	0.017	stream order at subbasin pourpoint	-2.016	.781	-2.579	0.049
	df	7					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Stratification by dominant geomorphology

Alpine-glaciated-dominant stratum (proportion in alpine-glaciated lands > .75; n=11)

Surveyed-length-scale response

Correlations were positive between surveyed-length-scale redd densities and subbasin proportion with slope >46% (r=.753, $p<0.01$), average aspect class (.667, $p<0.05$) and redd-surveyed channel slope (.636, $p<0.05$) in alpine-glaciated subbasins. Among candidate predictors, proportion with slope >46% correlated positively with redd-surveyed channel slope (.632, $p<0.05$), proportion with >32 inches precipitation (.642, $p<0.05$) and knickpoints below BAVS/stream km (.603, $p<0.05$), and negatively with road density (-.647, $p<0.05$). Redd-surveyed channel slope correlated positively with maximum-redd-density-reach channel slope (.922, $p<0.01$), and negatively with 1999 MWMT (-.852, $p<0.01$), brook trout presence (-.691, $p<0.05$) and stream order at pourpoint (-.657, $p<0.01$).

Steeper subbasin and channel slopes and more east-west stream orientation were associated with higher surveyed-length-scale redd densities in alpine-glaciated subbasins (Table 12). Simple regression models predicting redd densities from proportion with slope >46%, average aspect class and average redd-surveyed channel slope accounted for 57% (p=0.007), 44% (p=0.025) and 41% (p=0.035), respectively, of redd-density variation.

A multiple regression model predicting redd densities from average maximum air temperature (proportion of subbasin >50°F) and proportion of subbasin in volcanics explained 64% of the variation (p=0.017), but appeared entirely driven by a single subbasin (Figure 15, Table 12). Stony Creek had the only non-zero proportion of subbasin area within the volcanic geologic district (.057) in this stratum. Influence statistics for Stony could not be obtained, nor could the two-variable model be produced with Stony omitted, since volcanics proportion was constant (zero) for remaining subbasins in the stratum. A simple regression model predicting redd densities from proportion of subbasin area with average maximum air temperature >50°F was not significant (R^2=.200, p=0.168, n=11) unless Stony was omitted (R^2=.566, p=0.012, n=10). No other models meeting our significance, collinearity and overfitting criteria were found for this stratum with surveyed-length-scale redd densities.

Figure 15. Model 32. Maximum surveyed-length-scale redd densities (vertical axis) in relation to proportion with average maximum air temperature >50°F and proportion in volcanic geologic district in alpine-glaciated-dominant geomorphic stratum.

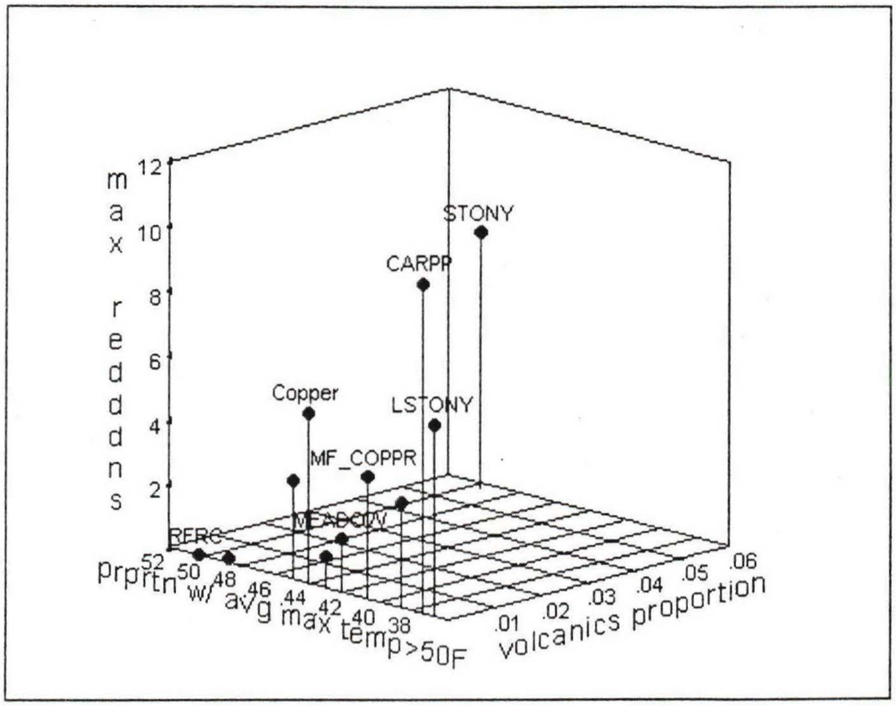


Table 12. **Most-significant regression models predicting maximum bull trout redds/surveyed stream length in alpine-glaciated dominant stratum of dominant geomorphology stratification (n=11).**

			Predictor variables	coefficient	std. error	t	p
Model 29	**R^2**	**.567**	**intercept**	**.271**	**1.254**	**.216**	**0.834**
	Adj. R^2	**.519**					
	F	**11.777**					
	p	**0.007**	**proportion subbasin area in slope classes >46%**	**23.654**	**6.892**	**3.432**	**0.007**
	df	**10**					
Model 30	R^2	.444	intercept	.830	1.375	.604	0.561
	Adj. R^2	.383					
	F	7.197					
	p	0.025	average aspect class (1=N-S, 10=E-W)	.683	.255	2.683	0.025
	df	10					
Model 31	R^2	.405	intercept	17.434	5.538	3.148	0.012
	Adj. R^2	.339					
	F	6.126					
	p	0.035	natural log average redd-surveyed channel slope	3.639	1.470	2.475	0.035
	df	10					
Model 32	R^2	.641	intercept	6.718	1.225	5.483	0.001
	Adj. R^2	.552	natural log (1+(proportion subbasin area w/ avg max air temp>50°F))	-22.717	7.034	-3.229	0.012
	F	7.152					
	p	0.017	proportion subbasin area in volcanic geologic district	139.725	44.535	3.137	0.014
	df	10					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Geologic stratification (by proportion subbasin area in granitics)

Low-granitics (< .1) stratum (n=9)

Surveyed-length-scale response

Average redd-surveyed channel slope was the only candidate predictor significantly correlated with surveyed-length-scale redd densities in low-granitics subbasins ($r=.765$, $p<0.05$). Among candidate predictors, correlations of redd-surveyed channel slope were negative with brook trout presence (-.876, $p<0.01$) and stream order at subbasin pourpoint (-.768, $p<0.05$), and positive with maximum-redd-density-reach average channel slope (.748, $p<0.05$).

Steeper average channel slopes were associated with higher redd densities in low-granitics subbasins. Average redd-surveyed channel slope alone accounted for 59% of surveyed-length-scale maximum redd density variation ($p=0.016$) (Table 13).

A model combining redd-surveyed channel slope and proportion in volcanic rock types explained 83% of the variation ($p=0.005$), but volcanics significance was entirely driven by a single highly-influential point (Stony Creek, Figure 16). Stony Creek had the highest maximum redd density in this stratum and was the only subbasin in the stratum with any volcanics (~6% of subbasin area), precluding use of influence statistics for Stony. Thus inclusion of volcanics proportion appeared to account for much of the redd-density variation unexplained by channel slope alone. The volcanic geologic district consisted of only a single polygon within the Rock Creek drainage, which straddled the Stony Creek/West Fork Rock Creek drainage divide. No similar apparent positive effect of volcanics was found in strata including the West Fork. We suspect volcanics significance in this model is largely an artifact of limited sample size in combination with the limited occurrence of volcanics in the drainage, rather than a "real" positive influence of volcanic rock types on redd densities.

Figure 16. Model 34. Maximum surveyed-length-scale redd densities (vertical axis) in relation to average redd-surveyed channel slope and proportion subbasin in volcanic geologic district within low-granitics stratum (untransformed variables shown).

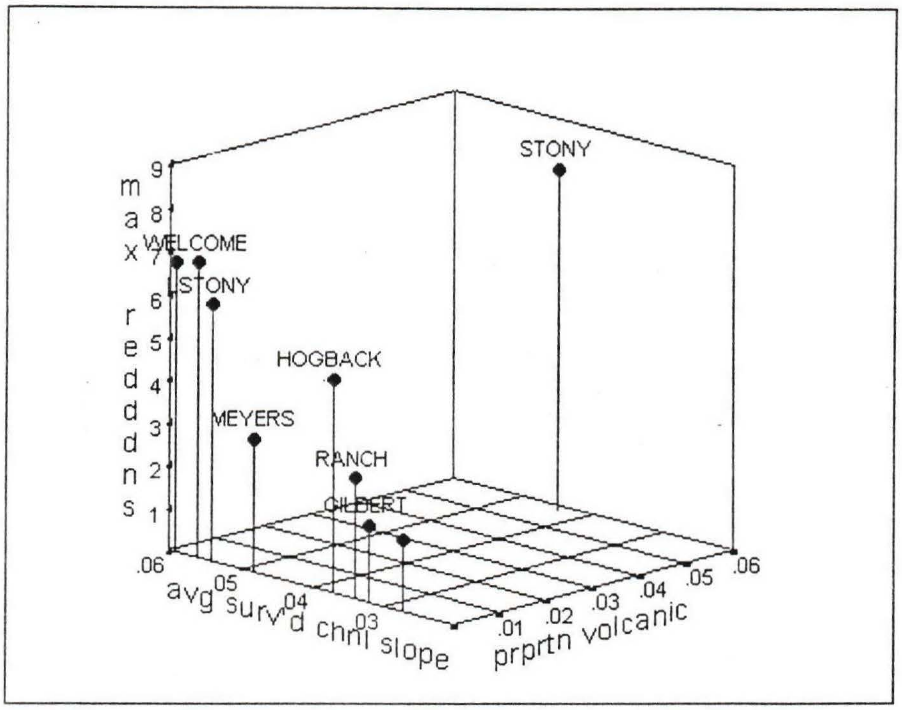


Table 13. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in low-granitics (<.1) stratum of geologic stratification (n=9).

			Predictor variables	coefficient	std. error	t	p
Model 33	R^2	.585	intercept	25.706	6.715	3.828	0.006
	Adj. R^2	.526					
	F	9.882	natural log average redd-surveyed channel slope	6.633	2.110	3.144	0.016
	p	0.016					
	df	8					
Model 34	R^2	.832	intercept	24.841	4.633	5.362	0.002
	Adj. R^2	.775	natural log average redd-surveyed channel slope	6.485	1.454	4.461	0.004
	F	14.805					
	p	0.005	proportion subbasin area in volcanic geologic district	62.530	21.121	2.961	0.025
	df	8					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Geologic stratification (by proportion subbasin area in granitics)

Higher-granitics (≥ .1) stratum (n=10)

Surveyed-length-scale response

In higher-granitics subbasins, surveyed-length-scale maximum redd densities were positively correlated with average subbasin elevation ($r=.838$, $p<0.01$), subbasin proportion with slopes >46% (.783, $p<0.01$) average redd-surveyed channel slope (.748, $p<0.05$) and knickpoints-below-BAVS/stream km (.655, $p<0.05$), and negatively with stream temperature ('99 MWMT) (-.643, $p<0.05$). All pairwise correlations among these candidate predictors were significant (range -.634 to .879, all $p<0.05$) except between average elevation and knicks-below-BAVS/km (.529, $p>0.05$), '99 MWMT and proportion slopes >46% (-.507, $p>0.05$), and '99 MWMT and knicks-below-BAVS/km (-.385, $p>0.05$).

Average subbasin elevation alone accounted for 70% ($p=0.002$) of the variation in surveyed-length-scale redd densities in higher-granitics subbasins (Table 14). Influence statistics suggested Carpp Creek might be influential in the regression. However, average elevation remained a significant predictor of redd densities even with Carpp omitted ($R^2=.461$, $p=0.044$, $n=9$).

Knicks-below-BAVS/km alone accounted for 43% of redd-density variation in higher-granitics subbasins ($p=0.040$). Influence analysis suggested possible influence of Carpp Creek and the Ross Fork above Falls Creek (Figure 17). Knicks-below-BAVS/km remained significant if Ross Fork above Falls Creek was excluded ($R^2=.549$, $p=0.022$, $n=9$), but not if Carpp ($R^2=.070$, $p=0.490$, $n=9$) or both ($R^2=.198$, $p=0.269$, $n=8$) were excluded. Significant simple regression models obtained with proportion with slope >46%, average redd-surveyed channel slope and '99 MWMT are not reported because influence statistics for one or more subbasins exceeded our criteria.

Figure 17. Model 36. Maximum surveyed-length-scale redd densities in relation to log (1+(knickpoints-below-BAVS/km)) in higher-granitics geologic stratum.

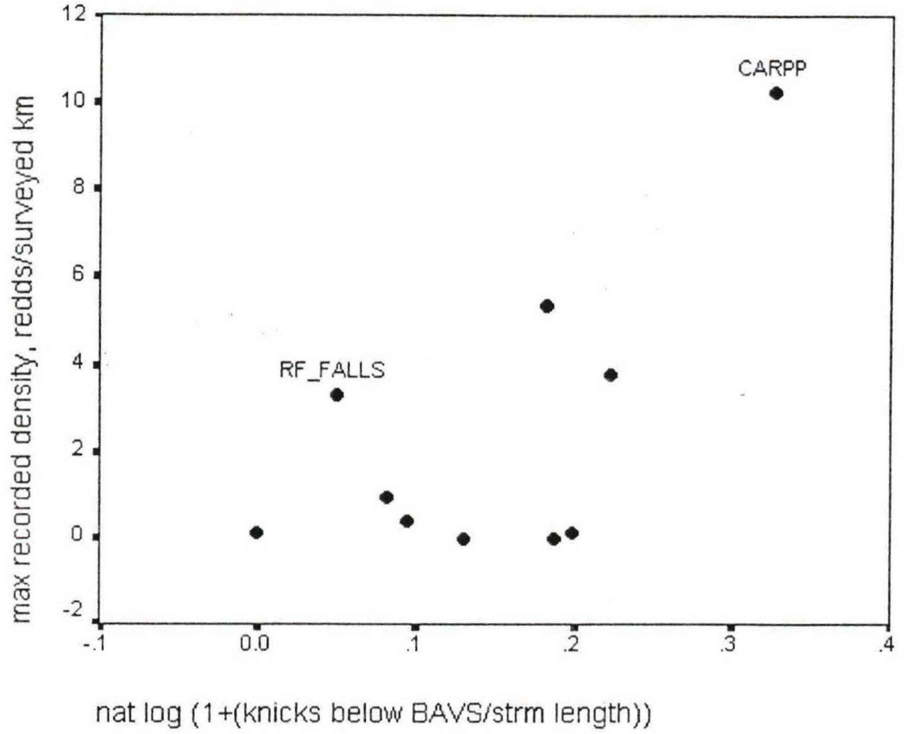


Table 14. Most-significant regression models predicting maximum bull trout redds/surveyed stream length in higher-granitics (≥ .1) stratum of geologic stratification (n=10).

			Predictor variables	coefficient	std. error	t	p
Model 35	**R^2**	**.702**	**intercept**	**54.224**	**13.077**	**-4.147**	**0.003**
	Adj. R^2	**.664**					
	F	**18.816**	**average subbasin elevation, feet**	**.007866**	**.002**	**4.338**	**0.002**
	p	**0.002**					
	df	**9**					
Model 36	R^2	.429	intercept	-.940	1.618	-.581	0.577
	Adj. R^2	.358					
	F	6.014	natural log (1+(knicks-below-BAVS/stream km))	23.005	9.381	2.452	0.040
	p	0.040					
	df	9					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Single-survey-reach redd density results

Unstratified sample

When redd densities were calculated at the scale of a single delineated redd-survey reach (finest scale permitted by the recorded data), the maximum value within a given subbasin ranged from zero (Bowles Cr. and Ross Fork below Falls Cr.) to 14.5 redds/km (Alder Cr.) (Table 3). Correlations of candidate predictors with reach-scale redd densities were generally similar but slightly weaker than with the surveyed-length-scale response, although average subbasin channel slope and 1998 MWMT were notable exceptions (Table 2). This resulted in many models using the same predictors as with the surveyed-length-scale response, though generally at lower significance. Here (including stratified results) we report only models that either used different predictors or crossed a higher significance threshold (i.e. model and all predictor coefficients' p<0.01) than with surveyed-length-scale redd densities.

While surveyed-length-scale redd densities correlated most strongly with surveyed-length-scale channel slope (among the three channel-slope scales examined), reach-scale redd densities correlated most strongly with the broadest-scale channel slope (average subbasin channel slope). Correlation of reach-scale redd densities with 1998 stream temperatures was stronger than with 1999 temperatures, the reverse of the surveyed-length-scale result. However, correlations of both years' temperature metrics with redd densities at both scales, as well as correlations between 1998 and 1999 temperatures (r=.951, p<0.01) were all highly significant (Table 2).

Only two (non-redundant) simple regression models using channel slope and stream temperature as predictors met our model-fitting criteria. Channel slopes averaged over the full extent of the routed hydrography in the subbasin (average subbasin channel slope) were positively associated with redd densities while 1998 MWMT was negatively associated with redd densities. Average subbasin channel slope alone explained 52% of the variation in maximum reach-scale redd densities (p=0.001). MWMT alone explained 40.5% of the variation (p=0.003) (Table 15).

Table 15. Most-significant multiple regression models predicting maximum bull trout redds/single maximum-redd-density reach length in 19 Rock Creek drainage subbasins.

			predictors	coefficient	std. error	t	p
Model 37	**R^2**	**.518**	**intercept**	**5.282**	**.912**	**5.794**	**<0.0005**
	Adj. R^2	**.490**					
	F	**18.301**	**natural log average subbasin channel slope**	**1.189**	**.278**	**4.278**	**0.001**
	p	**0.001**					
	df	**18**					
Model 38	**R^2**	**.405**	**intercept**	**3.968**	**.763**	**5.203**	**<0.0005**
	Adj. R^2	**.370**					
	F	**11.581**	**'98 MWMT + model-predicted for missing**	**-.176**	**.052**	**-3.403**	**0.003**
	p	**0.003**					
	df	**18**					

Bold denotes model and all predictor coefficients' $p < 0.01$

Stratified samples

Stratification by average subbasin channel slope
Lower-gradient (<5%) stratum (n=10 subbasins)
Single-survey-reach-scale response

No additional or higher-significance-threshold models meeting our significance, collinearity and overfitting criteria were found with redd densities summarized at the single-survey-reach scale within the lower-gradient stratum of average subbasin channel slopes.

Stratification by average subbasin channel slope
Higher-gradient (≥5%) stratum (n=9 subbasins)
Single-survey-reach-scale response

Average redd-surveyed channel slope ($r=.706$, $p<0.05$) and BAVS length ($r=.678$, $p<0.05$) both correlated positively with reach-scale redd densities in the higher-gradient stratum of average subbasin channel slopes. Among predictors, strong correlations of channel slope with stream order ($r= -.808$, $p<0.01$) and brook trout presence ($-.808$, $p<0.01$) were negative. BAVS length also correlated positively with knickpoints below BAVS/stream km ($r=.787$, $p<0.05$), proportion in precipitation classes >32" ($r=.772$, $p<0.05$) and trail density ($r=.687$, $p<0.05$), and negatively with distance to nearest bull trout spawning tributary ($r= -.690$, $p<0.05$).

Higher channel slopes and trail densities were associated with higher reach-scale redd densities in the most significant models from the higher-gradient subbasin channel slope stratum (Table 16). Average redd-surveyed channel slope alone accounted for 50% of the redd-density variation ($p=0.034$). Trail density in combination with channel slope explained 75% of the variation ($p=0.015$) (Figure 18).

Figure 18. Model 40. Maximum single-survey-reach redd densities (vertical axis) in relation to average redd-surveyed channel slope and trail density in higher-gradient stratum of average subbasin channel slopes (untransformed variables shown).

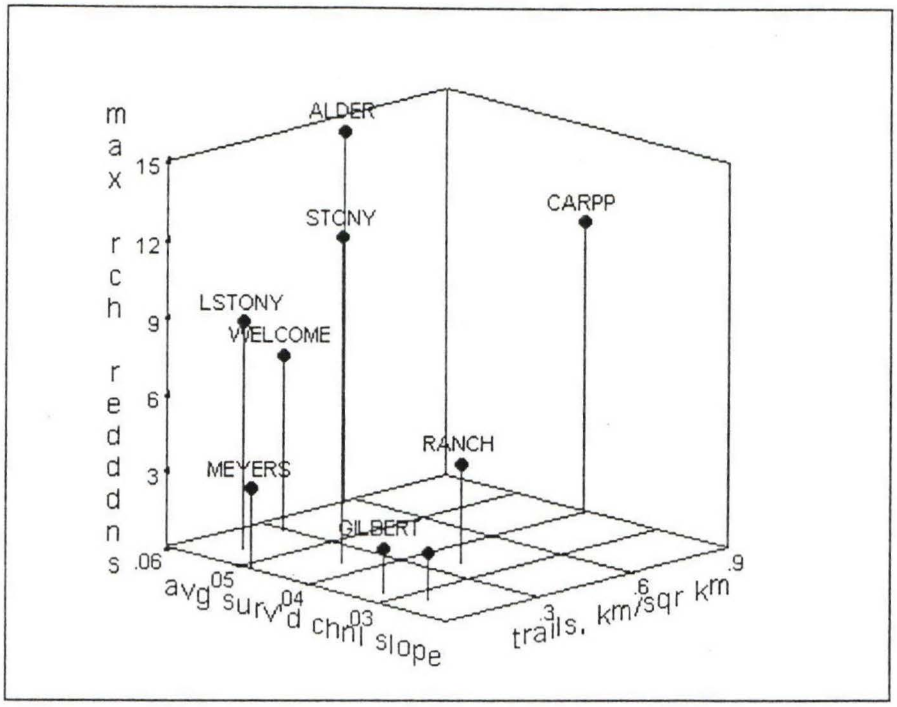


Table 16. Most-significant regression models predicting maximum bull trout redds/single maximum-redd-density reach length in higher-gradient (≥5%) stratum of average subbasin channel slopes (n=9). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 39	R^2 Adj. R^2	.498 .427	intercept	7.420	2.091	3.548	0.009
	F p df	6.957 0.034 8	natural log average redd-surveyed channel slope	1.738	.659	2.638	0.034
Model 40	R^2	.751	intercept	6.331	1.651	3.835	0.009
	Adj. R^2 F	.668 9.053	natural log average redd-surveyed channel slope	1.515	.509	2.975	0.025
	p df	0.015 8	natural log (1+(trail density, km/km^2))	1.680	.681	2.468	0.049

Bold denotes model and all predictor coefficients' $p < 0.01$.

Stratification by average redd-surveyed channel slope
Lower-gradient (<3%) stratum (n=10 subbasins)
Single-survey-reach-scale response

When redd densities were calculated for each individual redd-survey reach, maximum density within each subbasin again correlated significantly only with average subbasin elevation in this lower-gradient stratum, but the correlation was substantially stronger (r=.810, p=0.005) and the resulting model accounted for substantially more of the redd-density variation (66%, p=0.005) (Table 17). No other models fitting our criteria were found.

Table 17. Most-significant regression model predicting maximum bull trout redds/single maximum-redd-density reach length in lower-gradient (<3%) stratum of average redd-surveyed channel slopes (n=10). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 41	**R^2**	**.656**	**intercept**	**-16.797**	**4.542**	**-3.698**	**0.006**
	Adj. R^2	**.613**					
	F	**15.232**	**average subbasin elevation, feet**	**.002487**	**.001**	**3.903**	**0.005**
	p	**0.005**					
	df	**9**					

Bold denotes model and all predictor coefficients' p < 0.01.

Stratification by average redd-surveyed channel slope
Higher-gradient (≥3%) stratum (n=9 subbasins)
Single-survey-reach-scale response

Only the proportion of subbasin area in the fluvial-lacustrine geomorphic class correlated significantly with reach-scale redd densities in this stratum (r= -.677, p<0.05). This class consists of lands in the lower Rock Creek drainage and lower portions of its tributaries where valley fill deposition associated with inundation by Glacial Lake Missoula was the dominant geomorphic process (Jensen 1998). A marginally significant simple regression model predicting redd densities from fluvial-lacustrine proportion was discarded because influence statistics indicated it was driven by Gilbert Creek's lowest redd density in the sample and its fluvial-lacustrine proportion six times that of any other subbasin in the stratum (Figure 19). In a model also including proportion in a seedling/sapling classification from forest stand delineations as a predictor, fluvial-lacustrine proportion then appears to account for much of the unexplained variation from a non-significant positive correlation (r=.309, p=.419) between redd densities and seedling/sapling proportion. This results in a highly significant model with these two predictors, suggesting a positive effect of seedling/sapling proportion on redd densities that may nevertheless be meaningless or even misleading (Figure 19, Table 18). If Gilbert Creek is excluded from the sample, fluvial-lacustrine proportion is no longer a significant predictor (p=0.346), though the model remains significant (p=0.030). Influence analysis flags Carpp and

Meyers Creeks (though, somewhat surprisingly, not Gilbert) as possibly influential. Model significance increases greatly if Carpp alone (R^2=.953, p<0.0005, n=8), Meyers alone (R^2=.897, p=0.003, n=8) or both (R^2=.983, p<0.0005, n=7) are excluded, but Gilbert then again becomes highly influential. This highly unstable model behavior with inclusion or exclusion of individual subbasins suggests apparent significance of both fluvial-lacustrine proportion and seedling-sapling proportion may be largely an artifact of the confluence of the influences of those subbasins, rather than a real effect of either predictor on redd densities.

Figure 19. Model 42. Maximum single-survey-reach redd densities (vertical axis) in relation to proportions in fluvial-lacustrine geomorphic class and seedling/sapling forest stand classification in higher-gradient (≥3%) stratum of average surveyed channel slopes (untransformed variables shown).

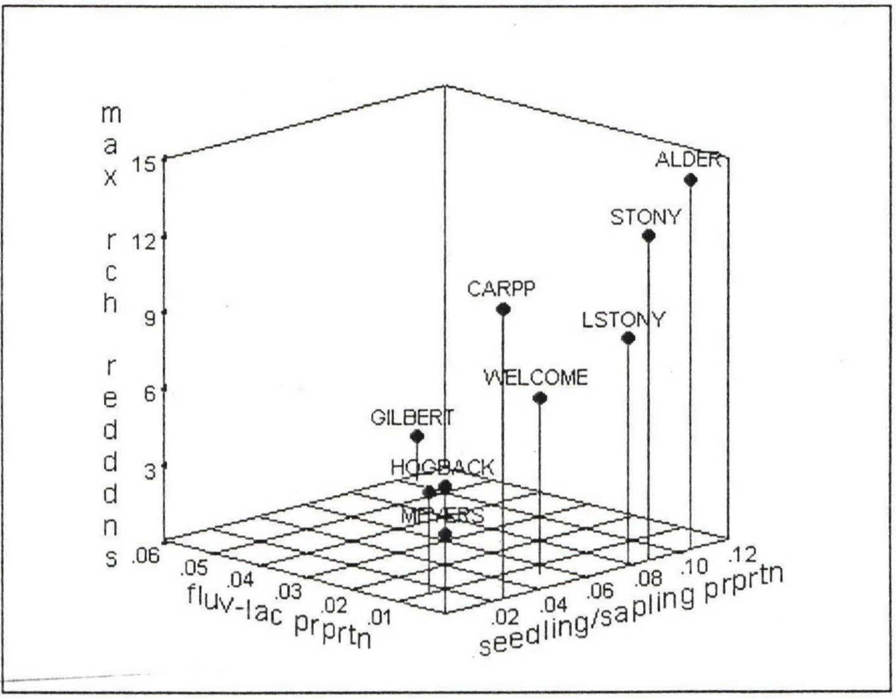


Table 18. Most-significant regression models predicting maximum bull trout redds/single maximum-redd-density reach length in higher-gradient (≥3%) stratum of average surveyed channel slopes (n=9). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 42	**R^2**	**.849**	**intercept**	**1.764**	**.143**	**12.316**	**<0.0005**
	Adj. R^2	**.799**					
	F	**16.856**	**proportion in fluvial-lacustrine class**	**-29.824**	**5.452**	**-5.471**	**0.002**
	p	**0.003**					
	df	**8**	**natural log proportion in seedling/sapling class**	**9.854**	**2.502**	**3.939**	**0.008**

Bold denotes model and all predictor coefficients' $p < 0.01$.

Temperature Stratification

1999 MWMT (+ model-predicted for missing) <13.3°C (n=9)

Single-survey-reach-scale response

Modeling maximum redd densities at the single-survey-reach scale produced two higher-significance-threshold models in the cool stratum (Table 19, Figures 20-22). Channel slope and trail density were again positively associated with redd densities, while association of stream temperature with redd densities was negative. The set of candidate predictors significantly correlated with the response was the same as with surveyed-length-scale redd densities, directions of correlations were identical and strengths of correlations were similar except that BAVS length correlation with reach-scale redd densities was not significant ($r=.617$, $p>0.05$). Average redd-surveyed channel slope and trail density together explained 92% of reach-scale redd density variation ($p<0.0005$) (Figure 20, Table 19). Trail density and stream temperature together explained 89% of the variation ($p=0.001$) (Figure 22).

Figure 20. Model 43. Single-survey-reach-scale maximum redd densities (vertical axis) in relation to average redd-surveyed channel slope and trail density in cooler stratum of stream temperatures (untransformed variables shown).

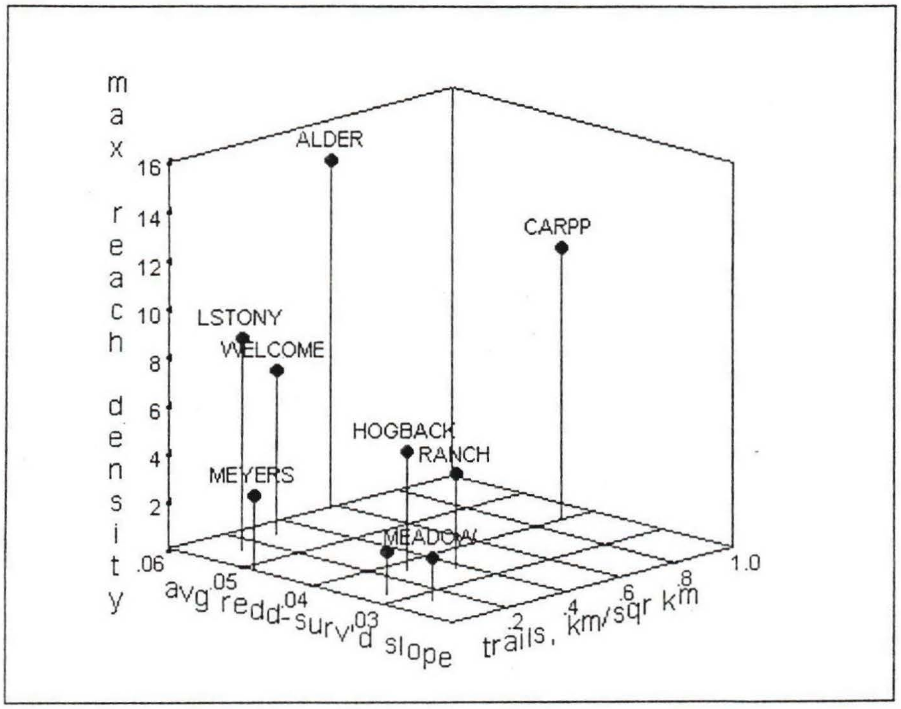


Figure 22. Model 45. Single-survey-reach-scale maximum redd densities (vertical axis) in relation to trail density and stream temperature in cooler stratum of stream temperatures (untransformed variables shown).

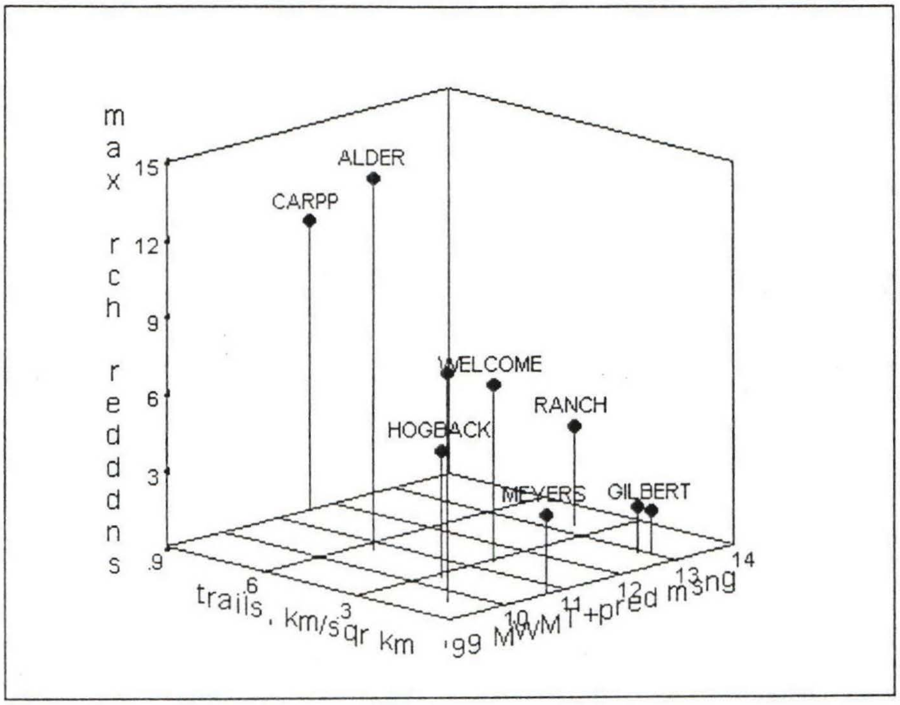


Table 19. Most-significant regression models predicting maximum bull trout redds/single maximum-redd-density reach length in cool (<13.3°C) stratum of 1999 MWMT (n=9). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 43	**R^2**	**.924**	**intercept**	**5.963**	**.835**	**7.139**	**<0.0005**
	Adj. R^2	**.899**	**natural log average redd-surveyed channel slope**	**1.438**	**.256**	**5.618**	**0.001**
	F	**36.603**					
	p	**<0.0005**	**natural log (1+trail density, km/km^2)**	**1.863**	**.349**	**5.342**	**0.002**
	df	**8**					
Model 44	**R^2**	**.894**	**intercept**	**9.471**	**1.795**	**5.276**	**0.002**
	Adj. R^2	**.858**	**natural log (1+trail density, km/km^2)**	**2.217**	**.406**	**5.457**	**0.002**
	F	**25.236**					
	p	**0.001**	**’99 MWMT (+ model-predicted for missing)**	**-3.357**	**.736**	**-4.559**	**0.004**
	df	**8**					

Bold denotes model and all predictor coefficients’ $p < 0.01$.

Temperature Stratification
1999 MWMT (+ model-predicted for missing) ≥ 13.3°C (n=9)
Single-survey-reach-scale response

No additional significant or higher-significance-threshold models meeting our significance, collinearity and overfitting criteria were obtained using reach-scale redd densities in the warmer stream temperature stratum.

Stratification by dominant geomorphology
Fluvial-dominant stratum (proportion in fluvial-dominant geomorphic class > .9; n=8)
Single-survey-reach-scale response

No higher-significance-threshold or additional significant models meeting our significance, collinearity and overfitting criteria were found for the fluvial-dominant geomorphic stratum with single-survey-reach-scale maximum redd densities.

Stratification by dominant geomorphology
Alpine-glaciated-dominant stratum (proportion in alpine-glaciated lands > .75; n=11)
Single-survey-reach-scale response

In contrast with the surveyed-length-scale response, redd densities at the survey-reach scale within the alpine-glaciated stratum correlated more strongly with average subbasin channel slope (r=.680, $p<0.05$) than with average redd-surveyed channel slope (.660, $p<0.05$). Stream temperature (1998 MWMT) correlated negatively (-.679, $p<0.05$) and subbasin proportion with slope >46% (.660, $p<0.05$) correlated positively with redd densities. Correlations among candidate predictors were negative between average subbasin channel slope and stream temperature (-.905, $p<0.01$), subbasin channel slope and subbasin area (-.854, $p<0.01$) subbasin channel slope and brook trout presence (-.648, $p<0.05$), and between proportion with slope >46% and road density (-.647, $p<0.05$). Correlations were positive between stream temperature and subbasin area (.761, $p<0.01$), stream temperature and brook trout presence (.707, $p<0.05$), and between proportion with slope >46% and proportion with precipitation >32" (.642, $p<0.05$).

Subbasin-scale channel slopes were positively associated with reach-scale maximum redd densities in alpine-glaciated subbasins, while stream temperature was negatively associated with redd densities. Simple regression models with average subbasin channel slope and 1998 MWMT as predictors each explained 46% (p=0.021 and 0.022, respectively) of reach-scale redd density variation in this stratum (Table 20).

Table 20. Most-significant regression models predicting maximum bull trout redds/single maximum-redd-density reach length in alpine-glaciated-dominant stratum of dominant geomorphology stratification (n=11). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 45	R^2	.463	intercept	6.497	1.798	3.613	0.006
	Adj. R^2	.403					
	F	7.750	natural log average subbasin channel slope	1.553	.558	2.784	0.021
	p	0.021					
	df	10					
Model 46	R^2	.461	intercept	4.194	.984	4.261	0.002
	Adj. R^2	.401					
	F	7.707	'98 MWMT (+ model-predicted for missing)	-.177	.064	-2.776	0.022
	p	0.022					
	df	10					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Geologic stratification (by proportion subbasin area in granitics)

Low-granitics (< .1) stratum (n=9)

Single-survey-reach-scale response

When summarized at the single-survey-reach scale, maximum redd densities were positively associated with stream length within BAVS and with trail density in lower-granitics subbasins (Table 21). Average redd-surveyed channel slope (r=.770, p<0.05) and stream length in BAVS (.707, p<0.05) were the only candidate predictors significantly correlated with reach-scale redd densities in this stratum. Stream length in BAVS alone explained 50% of redd density variation (p=0.033). BAVS length in combination with trail density accounted for 78% of the variation (p=0.010) (Figure 23, Table 21).

Figure 23. Model 49. Maximum single-survey-reach-scale redd densities (vertical axis) in relation to stream length within BAVS and trail density in low-granitics geologic stratum (untransformed variables shown).

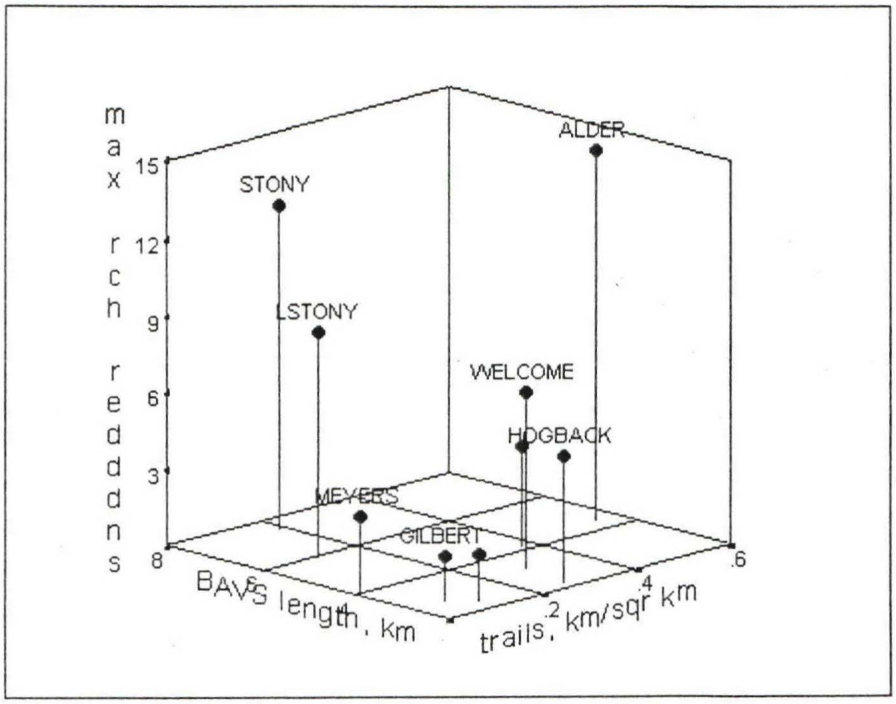


Table 21. Most-significant regression models predicting maximum bull trout redds/single max-redd-density reach length in low-granitics (<.1) stratum of geologic stratification (n=9). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 47	R^2	.500	intercept	-.351	.845	-.415	0.691
	Adj. R^2	.428					
	F	6.986					
	p	0.033	natural log (1+stream km in BAVS w/in subbasin)	1.401	.530	2.643	0.033
	df	8					
Model 48	R^2	.782	intercept	-.674	.613	-1.099	.314
	Adj. R^2	.709	natural log (1+stream km in BAVS w/in subbasin)	1.316	.379	3.473	0.013
	F	10.755					
	p	0.010	natural log (1+trail density, km/km^2)	2.475	.888	2.787	0.032
	df	8					

Bold denotes model and all predictor coefficients' $p < 0.01$.

Geologic stratification (by proportion subbasin area in granitics)

Higher-granitics (≥ .1) stratum (n=10)

Single-survey-reach-scale response

Modeling maximum redd densities at the single-survey-reach scale produced one additional model meeting our fitting criteria, in which both average subbasin channel slope and subbasin proportion in a seedling/sapling classification were positively associated with redd densities. The same three candidate predictors were positively correlated with reach-scale redd densities (average subbasin elevation, proportion subbasin slopes >46% and average subbasin channel slope) and strengths of correlations were similar to the surveyed-length scale (.868, $p<0.01$; .644, $p<0.05$; and .732, $p<0.05$, respectively). Correlations among the three predictors were identical to the surveyed-length-scale analysis (all $p<0.01$).

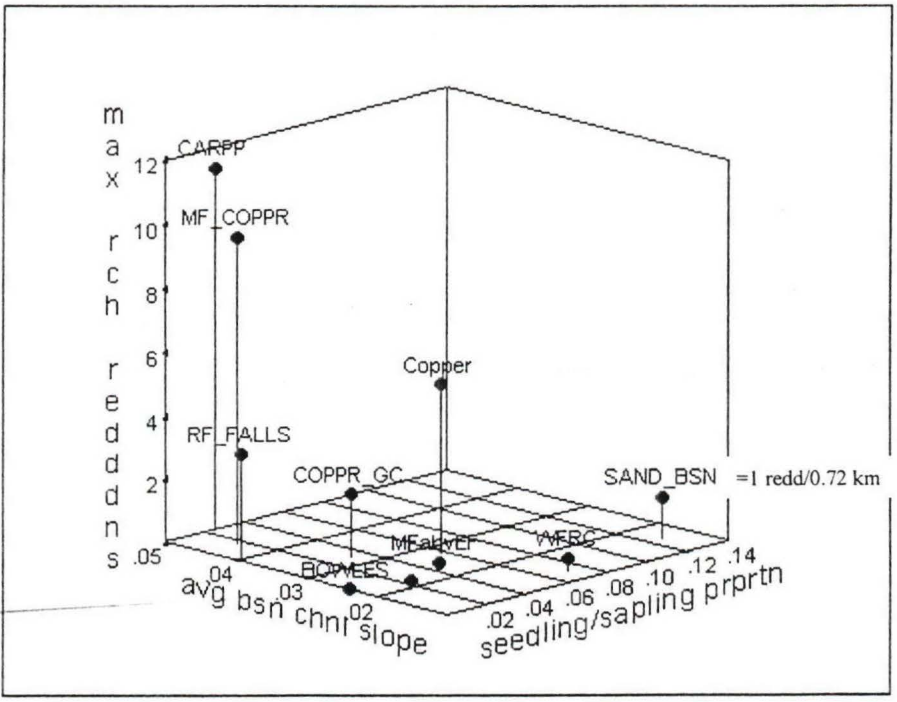
A multiple regression model including average subbasin channel slope and seedling/sapling proportion as predictors accounted for 82% ($p=0.003$) of the reach-scale redd density variation (Table 22, Figure 24). The non-significant pairwise correlation of seedling/sapling proportion with reach-scale redd density in this stratum was negative ($r= -.123$), but its apparent effect in this model (sign of coefficient) is positive. This appears to reflect a pattern of increasing redd densities with increasing seedling/sapling proportion within narrow ranges of subbasin channel slopes, i.e. when the stronger channel slope effect is already accounted for in the model (Figure 24). An anomalous, inflated reach-scale redd density for Sand Basin Creek (based on a single redd in only 0.45 mile surveyed of a 2.5-mile delineated survey reach in the only survey year) seems to magnify this apparent trend (Figure 24). Influence statistics suggest both Sand Basin and the West Fork (WFRC) may be influential. The model and both predictors remain significant if either WFRC alone ($R^2=.891$, $p=0.001$, $n=9$) or Sand Basin alone ($R^2=.835$, $p=0.005$, $n=9$) is excluded. However, if both are excluded, seedling/sapling proportion loses significance ($p=0.067$), although the model remains significant ($R^2=.892$, $p=0.004$, $n=8$).

Table 22. Most-significant regression model predicting maximum bull trout redds/single maximum-redd-density reach length in higher-granitics (≥.1) stratum of geologic stratification (n=10). Models redundant to surveyed-length-scale response omitted.

			Predictor variables	coefficient	std. error	t	p
Model 49	R^2	.817	intercept	10.084	1.620	6.225	<0.0005
	Adj. R^2 F	.765 15.647	natural log average subbasin channel slope	2.700	.487	5.542	0.001
	p df	0.003 9	natural log (1+proportion in seedling/sapling class)	19.910	6.060	3.286	0.013

Bold denotes model and all predictor coefficients' $p < 0.01$.

Figure 24. Model 50. Maximum single-survey-reach-scale redd densities (vertical axis) in relation to average subbasin channel slope and seedling/sapling proportion in higher-granitics geologic stratum (untransformed variables shown).



=1 redd/0.72 km

Table 23. Summary table of significant predictor variables in models predicting redd densities from landscape-scale attributes.

unstratified sample (n=19 subbasins) →	**surveyed-length-scale redd density response**		**single-survey-reach-scale redd density response**	
	+average redd-surveyed channel slope **-1999 MWMT** +maximum-redd-density-reach average channel slope +knickpoints-below-BAVS/stream km		**+average subbasin channel slope** **-1998 MWMT**	
stratification variable	**low** (fluvial for geormorphology)	**high** (alpine-glaciated for geomorphology)	**low** (fluvial for geormorphology)	**high** (alpine-glaciated for geomorphology)
average subbasin channel slope	+avg subbasin channel slope	**+BAVS length** +trail density +avg redd-surv'd chnl slope	---	+avg redd-surv'd chnl slope +trail density
average redd-surveyed channel slope	+average subbasin elevation	+BAVS length +trail density	**+avg subbasin elevation**	**-fluvial-lacustrine prprtn*** **+seedling-sapling prprtn***
1999 MWMT (+ model-predicted for missing)	**+trail density** **-stream order at pourpoint** +BAVS length -brook trout presence +avg redd-surv'd chnl slope +knicks-below-BAVS/km -1999 MWMT	+avg subbasin channel slope +proportion w/ slopes >46% +seedling/sapling proportion*	**+avg redd-surv'd chnl slope** **-1999 MWMT** **+trail density**	---
dominant geomorphic class	**+avg redd-surv'd chnl slope** **-1999 MWMT** -solar radiation -stream order at pourpoint	**+proportion w/ slopes >46%** +average aspect class +avg redd-surv'd chnl slope -prprtn w/ avg max air >50°F* +proportion in volcanics*	---	+avg subbasin channel slope -1998 MWMT
geology (proportion in granitics)	+avg redd-surv'd chnl slope +proportion in volcanics*	**+avg subbasin elevation** +knicks-below-BAVS/km	+BAVS length +trail density	+avg subbasin channel slope +seedling/sapling*

*Significance may be result of one or more influential/anomalous points.

Note: single-survey-reach-scale models redundant to surveyed-length-scale results not shown unless at higher significance threshold (all p<0.01).

Bold variable name indicates predictor in model with model p and all predictor variable coefficients' p<0.01.

+/- preceding variable name indicates sign of predictor coefficient in model.

DISCUSSION AND CONCLUSIONS

Stream temperature and channel slope variables most strongly and frequently correlated with among-stream varation in bull trout redd densities (Table 23). These variables are commonly cited as important determinants of bull trout habitat (e.g., Shepard 1985, Fraley and Shepard 1989, Rieman and McIntyre 1993). Valley morphology (number of knickpoints below BAVs within the drainage) also factored when redd densities were averaged over the entire surveyed stream length, but generally did not correlate with the maximum redd density metric. Overall we speculated that averaged reach redd density migth correspond more closely to overall capacity of the reach to support a population, whereas maximum reach redd density might reflect quality of the best available habitat. These two metrics may also differ in the vulnerability to observer error or bias, but this has not been sufficiently investigated.

The scale at which channel slope was measured—the slope of the maximum-density spawning reach, the average slope of all surveyed reaches, or the average slope of the entire channel network (subbasin channel slope) –determined the significance of its contribution to various regressions. When the response variable was average redd density of all surveyed reaches, the average slope of the corresponding reaches was most strongly correlated, with a weaker but significant association with slope of the maximum-density reach. Single-survey reach maximum density response variable, however, was best correlated with the larger subbasin scale slope measurement. The relative position of these variables switched among the different stratified analyses, with little obvious explanation. All of these relationships suggested redd density increased with channel slope among sites, which appears contrary to literature reports that bull trout spawning favors the lowest-gradient reaches (e.g., Fraley and Shepard 1989). In Rock Creek, spawning is definitely more concentrated in reaches near 2 percent slope or greater, where substrates are dominated by coarsely bedded cobbles, and fines are rare. Streams of gentler slope in Rock Creek tend to be rich in fines, and may be preferentially impacted by livestock or roads, in ways our data did not measure.

Management–related variables, including road density, but with the exception of density of trails in the watershed, did not consistently or strongly correspond with redd abundance in Rock Creek drainage. Redd density was consistently and positively associated with primitive trials. Trails were included in the analysis simply because the data were available and linked to road density information (trail density inversely related to road density). We are uncertain what causal basis there may be for trail density influencing bull trout abundance, and suspect it may be in indirect association, with the presence of trails reflecting undeveloped backcountry, topographic complexity, or some other feature of landscapes that is associated with benefits to bull trout. Trails may be associated with human access to spawning areas in some cases, but unlike roads, most trails in Rock Creek are located in near-ridge and headwater positions, far from bull trout habitat.

Brook trout presence was negatively associated with redd density only among colder streams. The proportion of seedling/sapling seral stage (presumed to be an indicator of logging disturbance) was positively correlated with redds among warmer streams and those with a high proportion of alpine-glacial terrain. We caution that this relationship is weak and variation in redd density among the warmer streams is quite small (all densities are relatively low), so that this relations may result from, or at least is prone to alteration by, survey error. Additionally, some seedling/sapling stands, especially at higher elevations, may originate from snow avalanches or other natural processes.

Within the colder stream category, water temperature variation explained further variation in redd density. However, in the warmer stream category, temperature did not weigh in. This suggests that water temperature increases in the coldest streams might have a much greater proportional impact on bull trout than warming of streams that are already relatively warm. Also among the colder streams, redd density declined as stream size (order) increased, and average survey reach channel slope decreased.

Relationships with geomorphic and geologic variables were inconsistent and not straightforward to interpret.

In general, stratified analyses did not improve correlations, but did sometimes change which additional variables weighed in most strongly. Our samples sizes grew small in stratified analyses, and this reduces the confidence one might have in the models resulting from them. No simple model or rules for classifying streams emerged from our sudy, and error that influenced the results with small sample sizes may drive this. However, it is also possible that bull trout respond contingently to host of conditioned factors, as Watson and Hillman suggested (1997). However we can conclude that stream temperature (a variable that was inadequately capture in Watson and Hillman's data) and stream channel slope are very important determining variables. Our results also indicate that channel slope relations are not simple and linear, and this warrants further careful investigation to ferret out causal factors involved. Models to predict bull trout response to physical variables may need to be empirically tuned to local circumstances. There is as yet no reason to assume that a single simple classification of stream or landtype will explain a useful proportion of bull trout variation, although relationships with water temperature are consistent, with many studies in the US portion of the bull trout's range, including this one, point to the importance of the coldest extant streams (as measured in summer) as centers of bull trout abundance and reproduction. BAV's variables measuring valley morphology that influences hyporheic flow exchange (Baxter 1997, Baxter et al. 2000) were prominent both in Rock Creek and in the Swan basin study, and the influence of vertical flow exchange is highly correlated with thermal regime (Baxter 1997).

Why didn't road density or other land use variables weigh heavily in these data? Baxter et al. (2000) showed a similar magnitude of variation in abundance of redds associated with road density as we observed for temperature, channel slope, and occasionally other natural factors in Rock Creek. We were surprised at the lack of apparent management influence, until we stepped back and looked at the relative level of human disturbance in Rock Creek compared to the Swan Basin sites. Road density in the Swan tributaries ranged from 0.94 to 12.13 km/km^2, whereas among Rock Creek tributaries it varied from 0 to 1.49 km/km^2. In essence, all of the Rock Creek tributaries in our sample (i.e., all of those with known consistent spawning of bull trout) are lightly roaded compared to regional average conditions. Another possible reason is that we were able to locate no GIS metric that directly quantified grazing or mining activity or impact. Grazing probably outweighs logging or even roads in terms of impact to stream habitat in the Rock Creek Basin, especially in the upper basin where bull trout are more concentrated. More work is warranted to determine if regional trends would emerge from the apparent complexity evident in this intra-basin study.

If there is a "master variable" explaining bull trout abundance in a wide variety of settings across disparate scales, it appears to be temperature. Previous models of bull trout occurrence (Reiman and Dunham 1999) and of climate change effects on trout distribution (Keleher and Rahel 1996) have assumed that elevation is a predictor of stream maximum temperature. We believe this is a faulty assumption, which may have critical consequences for scaling up to regional models. Among Rock Creek tributaries harboring bull trout, summer maximum water temperature increases with elevation--the opposite of the presumed relationship. In this area, local climate, topography, and possible groundwater hydrology and land use appear to play a much larger role in determining stream temperature than does elevation per se.

Watson and Hillan (1997) suggested that generalizing about bull trout habitat requirements is difficult or infeasible due to unspecified "hierarchical" contingencies in habitat selection. While habitat selection may indeed be an actively or passively hierarchical process, we think there are several other possible reasons why Watson and Hillman's results proved realtively inscrutable: 1)their analysis was based primarily on bull trout presence v. presumed absence; our analysis looks at abundance responses across habitat gradients and is insensitive to error in always-problematic absent v. rare determinations; 2) they lacked adequate data on thermal regimes, whereas we had comprehensive continuous records of summer stream temperature for most sites; 3) their study area was heavily altered and impacted by human activity, whereas Rock Creek is only modestly affected. Where streams are impacted by numerous human disturbances, biological responses are likely to be complicated and difficult to diagnose. As a caveat, we should note that both Watson and Hillman and our study lacked winter temperature data, and Jakober et al. (1998) recognized the potential importance of this factor to bull trout ecology.

We believe that with a critical eye toward accommodating data limitations, exploratory empirical studies of this kind are useful and necessary to inform the development of useful regional models of population status and effects of land and water management on population viability, injury, or recovery. Refinement will depend most importantly on the expanded availability of high-quality data for redd counts or other biological response metrics. Suitable time series of redd counts might add substantial analytic power and increase confidence in the inferences in this study (e.g., Reiman and McIntyre 1996, Baxter et al. 2000), but by and large we suspect that the spatial distribution, or number of streams for which data are available, is the more limiting factor for this kind of study. Uncertainty about the accuracy of the counts also bears resolution Dunham et al. 2001) .

Certain potentially important environmental data are also lacking, and efforts ought to be made to develop appropriate spatial coverages for grazing and mining impact, and the spatial extent of logging disturbance. Water temperature is also a difficult but important variable to map, there is virtually no spatial data coverage or predictive mapping available for water temperature. We measured water temperature in the field at most sites, then estimated the missing temperature stations after developing a prediction model based on the known sites (Carnefix and Frissell, in prep.). Simple elevation-based models of water temperature as used in previous studies may not be justified, and winter thermal data (often correlated with summer regimes) may be equally important.

Researchers should also give more attention to the consequences of measurement scale for channel slope, as our analysis suggests the possibility that the consequences of channel slope for the productivity of a reach may be dictated by the slope of a valley segment, stream network or catchment within which it is embedded. Finally, explicit attention should be paid to certain strongly contingent relationships observed in these analysis, such as the apparent interaction between channel and basin slope that, if it proves to be consistent, might provide a useful tool for classifying streams in terms of sensitivity or productivity. If Watson and Hillman (1997) are correct, such contingencies are so variable and complex that no generalizations are possible. We caution that it is important to account for sampling error and weak statistical power as a consequence of small sample size before favoring such null hypotheses. We are not so pessimistic, and we suggest our results provide reason to expect that despite probable error, certain variables (such thermal regime, channel slope, and BAV structure) have broadly consistent predictive power, when adequately resolved data are available.

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